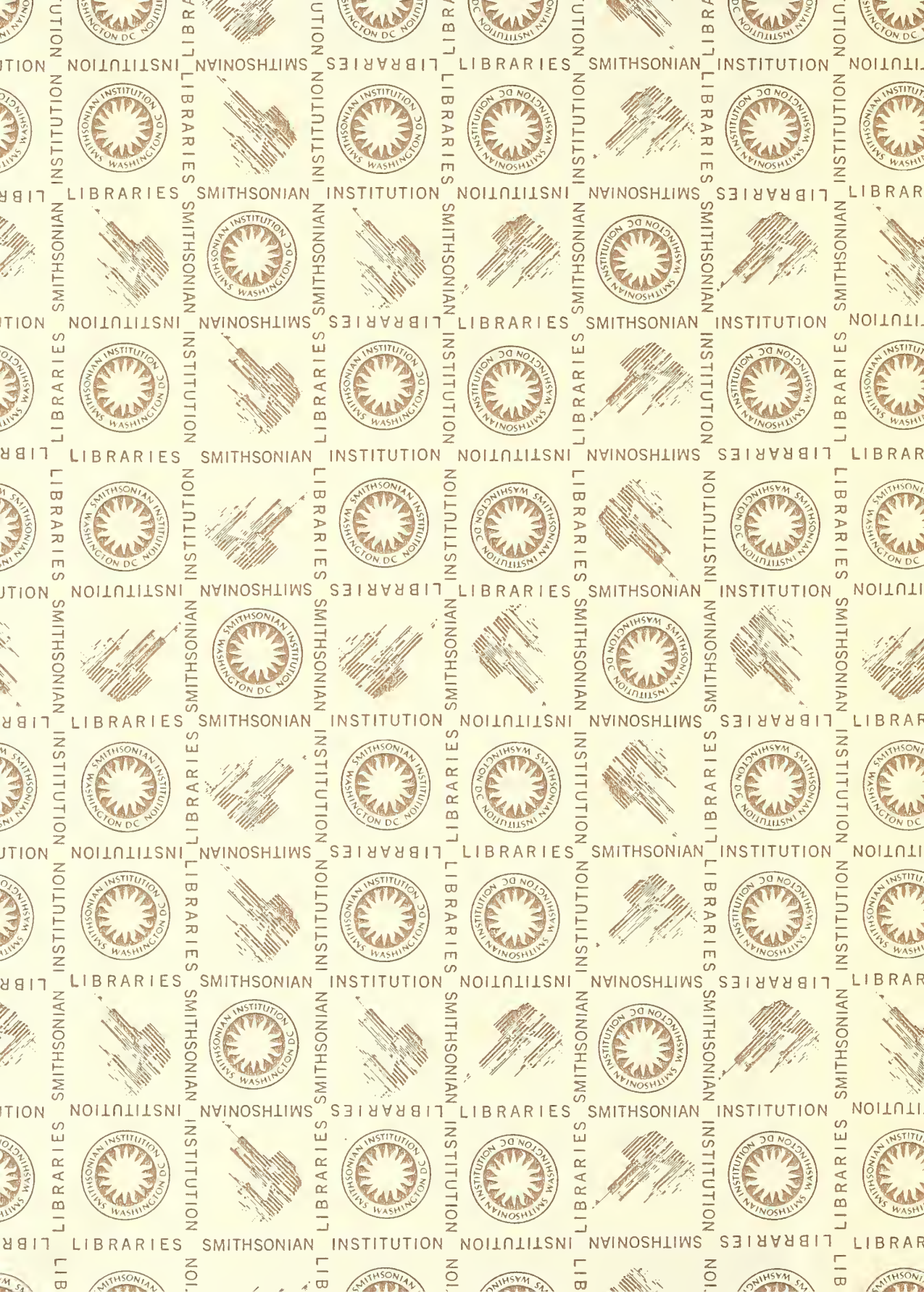






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THE UPPER CAMBRIAN TRILOBITE *IRVINGELLA NUNEATONENSIS* (SHARMAN)

by A. W. A. RUSHTON

ABSTRACT. *Irvingella nuneatonensis* (Sharman 1886), of which the complete dorsal exoskeleton is known, is redescribed, illustrated for the first time, and distinguished from other species. The ventral cephalic sutures and rostrum are like those of *Dunderbergia* (family Elviniidae). Three abnormally developed individuals are described. *I. nuneatonensis* comes from the upper part of the Zone of *Olenus* (above the base of the Subzone of *Olenus dentatus*) and its horizon is not below the upper part of the *Elvinia* Zone of the Upper Cambrian sequence in the U.S.A.

IN the course of the Geological Survey's investigation of the pre-Carboniferous rocks in the neighbourhood of the Warwickshire coalfield in the English Midlands (Strahan 1886), several specimens of a trilobite were collected from the Upper Cambrian shales ('Lower Silurian' in the original account) exposed in the Midland Railway Cutting between Nuneaton and Stockingford; they were described by Sharman (1886, p. 565) as a new species, *Olenus nuneatonensis*. Lapworth (1898, p. 347), apparently recognizing that the species was not a true olenid, referred to it as 'an Olenoid form, *Olenus* (?) *nuneatonensis*', but its affinities were not made known until Stubblefield (1932, p. 65) assigned it to the genus *Irvingella* Ulrich and Resser (*in* Walcott 1924). Palmer (1965, pp. 20–21, 45–46) showed that *Irvingella* is a widely distributed genus, and is a useful index for inter-continental correlation since it has a short stratigraphical range; *I. nuneatonensis* is of particular importance in this connexion because it provides the clearest evidence so far found for the stratigraphical position of *Irvingella* in the Upper Cambrian succession of Europe, correlation of which with the coeval succession in the United States of America is notoriously difficult. *I. nuneatonensis* is also of interest in being the only described species of the genus in which the rostrum and entire thorax are known.

The techniques and terminology employed in this study are the same as those given by the writer in an earlier work (Rushton 1966); in particular it should be noticed that the occipital and glabellar furrows are referred to respectively as S0, S1, S2, etc. (counting from the back forwards), and the occipital ring is excluded from the glabella.

Genus *IRVINGELLA* Ulrich and Resser *in* Walcott 1924

Type species, by original designation. *Irvingella major* Ulrich and Resser *in* Walcott 1924.

The genus *Irvingella* has been discussed by Palmer (1960) and Öpik (1963), and the species of the genus were reviewed by Palmer (1965), who considered the following valid: *I. major* Ulrich and Resser, *I. angustilimbatus* Kobayashi, *I. flohri* Resser, *I. suecica* Westergård, and *I. transversa* Palmer, and, with some doubt, *I. nuneatonensis* (Sharman), *I. platycephala* Rusconi, and *I. tropica* Öpik; he reserved comment on *I. taitzehuensis* Lu, *Komaspis* (*Parairvingella*) *convexa* Kobayashi, and *K. (P.) megalops* Kobayashi.

[*Palaeontology*, Vol. 10, Part 3, 1967, pp. 339–48, pl. 52.]

According to Kobayashi (1954 and elsewhere) *Irvingella* is a genus of the Komaspidae, which family he regarded as descended from a relative of the genus *Bathynotus* Hall. However, as discussed by Öpik (1963, pp. 94, 95) and Palmer (1960, p. 73), the concept of the Komaspidae, based upon the inadequately known *Komaspis* Kobayashi (type species *K. typa* Kobayashi), is of doubtful value, and Palmer has advocated the grouping of *Irvingella* with the ptychopariacean family Elviniidae, suggesting that *Elviniella laevis* Palmer is the direct ancestor of the *Irvingella* species in the Great Basin region of the U.S.A. (Palmer 1965, p. 20). This idea receives some further support from the discovery that the rostrum and ventral sutures in a species of *Irvingella* (text-fig. 1b) are exactly like those of *Dunderbergia* (Palmer 1960, p. 64, fig. 8c), the latter being a genus of the Elviniidae and possibly directly related to *Elvinia* itself (Palmer 1965, p. 17); the ventral cephalic sutures of *Bathynotus* have a different ('Bathynotid') pattern (Harrington *et al.* 1959, p. O65, fig. 48 I and p. O67), and according to Lochman (1953, p. 890), the Bathynotidae are not related to *Irvingella*.

Irvingella nuneatonensis (Sharman 1886)

Plate 52, figs. 1–12; text-figs. 1, 2

- 1886 *Olenus Nuneatonensis* Sharman; Strahan, p. 548. (*Nom. nud.* in list).
- 1886 *Olenus Nuneatonensis*; Sharman, p. 565 (described, no figure).
- 1898 *Olenus* (?) *nuneatonensis* Sharman; Lapworth, pp. 347, 348 (mentioned and listed).
- 1932 *Irvingella nuneatonensis* (Sharman); Stubblefield, p. 65 (species transferred to *Irvingella*).
- 1954 *Irvingella nuneatoneusis* (Sharman 1886 [*sic*]), [also attributed to 'Shorma (1731)']; Kobayashi, pp. 25, 27, 35, 41 (remarks, listed).
- 1965 *Irvingella nuneatonensis* (Sharman); Palmer, p. 46 (mentioned as possibly distinct from *Irvingella major*).

Material. Sharman's original material was all collected from one locality and is in the collection of the Institute of Geological Sciences (formerly Geological Survey and Museum), nos. GSM 50280–6,

EXPLANATION OF PLATE 52

Irvingella nuneatonensis (Sharman 1886).

Fig. 1a–d. Cranidium, GSM 50285–6. a, dorsal view (latex cast); b–d, dorsal, lateral, and anterior views. $\times 2.5$.

Fig. 2. Cranidium showing palpebral lobe, GSM JR3134. $\times 2.5$.

Fig. 3a–d. Cranidium, GSM JR3137. a, dorsal view with S3 distinct; b, left side viewed obliquely from above; c, anterior view showing supposed S4; d, right lateral view. $\times 2.5$.

Figs. 4, 5. Immature cranidia showing anterior border, GSM JR3143, GSM 50282. $\times 5$.

Fig. 6. Small axial shield, GSM 50283. $\times 5$.

Fig. 7. Thorax of small individual with two free cheeks (slightly retouched), GSM 50284. $\times 5$.

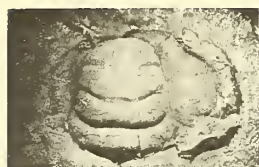
Fig. 8. Lectotype, small dorsal shield with free cheeks displaced (slightly retouched), GSM 50280. $\times 5$.

Fig. 9a, b. a, Pygidium, posterior part of thorax and ventral aspect of a free cheek (latex cast), GSM JR3126; b, the same free cheek, lateral (abaxial) view of interior surface. $\times 2.5$.

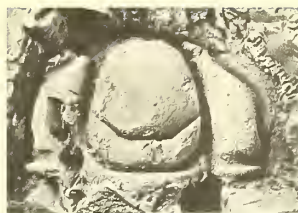
Fig. 10a–c. Part of thorax and pygidium, GSM JR 3125 (counterpart of JR3126, fig. 9). a–c, dorsal, lateral, and posterior views. $\times 2.5$.

Fig. 11. Complete thorax with deformed pygidium, GSM JR3127 (latex cast). $\times 2.5$.

Fig. 12a, b. Fragment of thorax and pygidium, GSM JR3149. a, b, dorsal and posterior views. $\times 2.5$. All the specimens are in the collection of the Institute of Geological Sciences (formerly Geological Survey and Museum) and are internal moulds unless otherwise stated; for locality see text. All photographs by the writer; specimens whitened before photography except that in fig. 7, which was taken under alcohol.



1a



2



3a



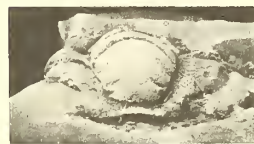
3b



1b



1d



3c



3d



1c



4



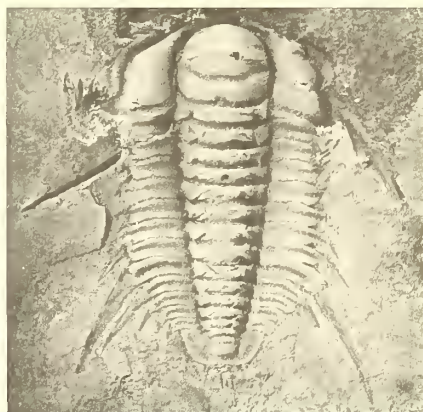
5



6



7



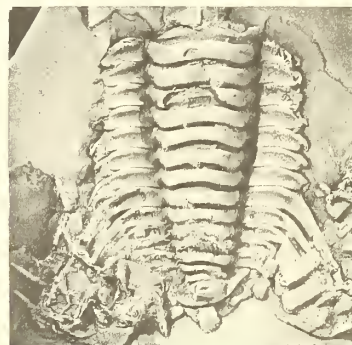
8



9a



10a



11



9b



10c



12a



10b



12b

JR3120-44, and JR3147-9. It consists of fragments of twenty-eight specimens including one dorsal shield (the lectotype), one axial shield, a cephalon, about six useful cranidia, and three or four fairly complete examples of the thorax, mostly with the pygidium attached. At a different locality the writer collected a small axial shield associated with part of a very large thorax, part of another thorax and a small pygidium with three thoracic segments attached; these specimens, thought to be of this species, are in the collection of the Sedgwick Museum, Cambridge, Nos. SM A57283-6.

All the specimens are preserved as internal and external moulds in grey or greenish silty and slightly micaceous shale. Much of their original convexity is preserved, the exoskeleton being thick and strong, but there are cracks in some of the specimens (e.g. Pl. 52, fig. 1*b*, in the occipital ring; fig. 3*a*, in the left cheek) which are probably due to the compression of compacting sediment. Morphologically, their effect is to increase the width and reduce the convexity of the affected part in relation to other parts. The lectotype has suffered adventitious frontal pressure which has fractured and foreshortened the cranidium, as stated by Palmer (1965, p. 46).

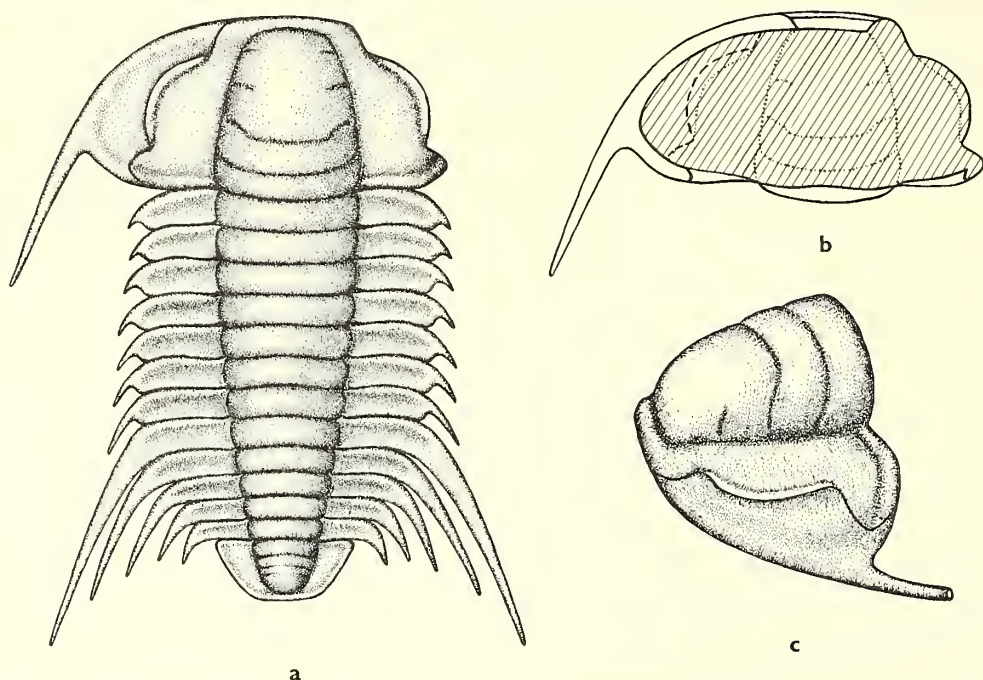
Lectotype. The lectotype is the small dorsal shield described by Sharman, GSM 50280 (Pl. 52, fig. 8).

Diagnosis. A species of *Irvingella* with a tapered glabella, the second and third pairs of lateral glabellar furrows (S2 and S3) distinct, the frontal area undivided in holaspide cranidia more than about 2-3 mm. long, the anterior ends of the eyes further apart than the width of the occipital ring, and interocular cheeks about half as wide as the glabella across a line through the anterior ends of S1.

Description. Cranidium approximately semicircular, convex in mature individuals. Cephalic axis long, tapering forwards, roughly parabolic in outline, slightly truncate in front but with the anterolateral corners rounded, strongly convex longitudinally and moderately convex transversely; the width is about five-sixths of the length. S1 deep, wide, lateral parts oblique backwards and slightly convex forwards, joined across the glabella by a transverse median portion; S2 distinct, less oblique, convex forwards, short; S3 nearly transverse, convex forwards, weak on external moulds but distinct on internal moulds, short; one specimen, GSM JR3137 (Pl. 52, fig. 3*c*), has a pair of pits which may represent S4. Occipital ring about one-sixth of the cephalic axial length. S0 deep, simple, concave forwards. In smaller specimens the glabella is relatively narrow and less convex.

Frontal area short, one-tenth or less of the cephalic axial length, bending down vertically in front. Two small cranidia (Pl. 52, figs. 4, 5, about 2.5 and 2.0 mm. long respectively) have a relatively longer frontal area divided into a preglabellar field and anterior border—a feature of immaturity, as in some other species of *Irvingella* (Palmer 1965). Preocular cheeks narrow. Interocular cheeks fairly flat, widening backwards, the width from the axial to the palpebral furrow at the level of the anterior ends of S1 just over half the glabellar width at the same level. Postocular cheeks short, bent down abaxially, mostly occupied by the posterior border and furrow. Smaller specimens have relatively wider cheeks. Palpebral furrow shallow. Palpebral lobe long, its chord two-thirds or less of the length of the cephalic axis; depressed below the level of the interocular cheeks, curved (most sharply near the mid-length), and horizontal except at the ends which are bent abruptly down through a right angle; anterior ends opposite S3 and situated slightly further apart than the greatest width of the cephalic axis. Preocular facial sutures very short, converging forwards, just submarginal in front of the glabella. Postocular sutures divergent with a downward course behind the eye, curving inwards and upwards again across the posterior border, continuing adaxially for a short distance before curving forward to cut the doublure (text-fig. 1*b, c*).

Free cheeks narrow anteriorly, wider behind, with straight spine which is almost round in cross-section; ocular surface steep; border-furrow weak or absent. Doublure curled under, tube-like (a feature of the Elviniidae; cf. Palmer 1960, p. 64), extended adaxially beyond the dorsal surface at both ends (Pl. 52, figs. 9*a*, *b*; text-fig. 1*b*). One cephalon (GSM JR3121) shows that the rostrum is about as wide as the anterior part



TEXT-FIG. 1. (a) Reconstruction of *Irvingella nuneatonensis* (Sharman), $\times 4$ approx.; (b) Diagram of the ventral aspect of the cephalon, showing rostrum; (c) Sketch of side-view of a young cephalon, $\times 8$ approx.

of the glabella and is slightly less long sagittally than the doublure of the free cheeks (text-fig. 1*b*). Hypostome not known.

Thorax of twelve segments, parallel-sided for the first seven, the eighth segment macropleural, the remainder narrowing to the pygidium. Axis convex, broad anteriorly, narrowing evenly behind. Anterior pleura about half as wide as the axis with a short spine springing from the anterior edge; in the second to seventh segments the pleurae are progressively wider and the spines longer. The spines on the remaining pleurae are broad and strong; the macropleurae on the eighth segment extend back to or beyond the pygidium, but the spines on the ninth to twelfth segments are progressively shorter.

Pygidium small, trapezoidal, about twice as wide as long. Axis occupies half the total width and most of the length of the pygidium, strongly convex, rounded and almost vertical behind, in larger specimens composed of three rings of which the last is only weakly marked off from the terminal part; in smaller specimens there are only two rings besides the terminal part. Pleural regions flat, furrowed obscurely or unfurrowed but

with a narrow, weakly marked border. In rear view the posterior margin is slightly arched (Pl. 52, fig. 12*b*).

The exoskeleton was up to 0.1 mm. thick and was fairly rigid (see under 'Material', above). From the form of the cracks which have affected some specimens, however, it may be inferred that it was not brittle but slightly flexible. Some of the best-preserved external moulds show that the exoskeleton was minutely granulose.

Measurements in mm.

<i>GSM specimen no.</i>	50282	50283	50280	<i>JR</i> 3137	50285	<i>JR</i> 3134	<i>JR</i> 3127	<i>JR</i> 3125-6
Length of cephalic axis	1.5	2.4	2.8 ¹	6.4	6.9	8.1	—	—
Width of occipital ring	0.9	1.7	2.5	5.0	5.7	6.7	—	—
Width of glabella at S1	0.9	1.6	2.4	4.3	4.7	6.0	—	—
Width of interocular cheek	0.6	1.1	1.2	2.2	2.4	3.2	—	—
Length of frontal area	0.35 ²	0.3	—	0.6	0.6	—	—	—
Chord of palpebral lobe	1.0	1.7	2.2	3.9	—	5.1	—	—
Length of thorax	—	4.5	5.5	—	—	—	12.5	—
Length of pygidium	—	0.7	1.0	—	—	—	2.3 ³	2.9
Width of pygidium	—	1.5 ⁴	2.2	—	—	—	—	6.8

¹ Foreshortened by frontal pressure.

³ Teratological pygidium.

² Preglabellar field with anterior border.

⁴ Estimated figure.

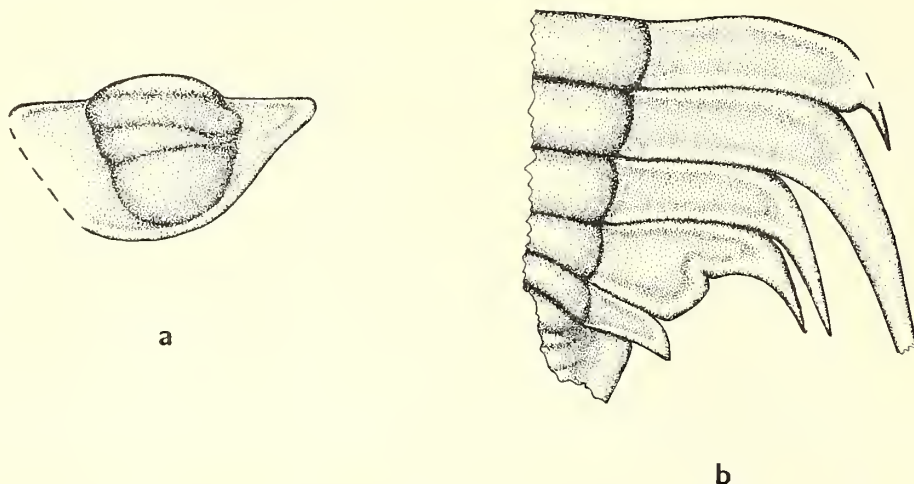
The axial length of the lectotype (GSM 50280) is 9.3 mm. but before deformation it was probably about 9.6 mm. The largest specimen (SM A57283) has a thoracic axis 12.5 mm. wide, suggesting a total length for the whole trilobite of 40–50 mm.

Remarks. In general, Sharman's description is accurate, but the statement that the glabella bends over the anterior margin applies only to the lectotype, which has been affected by frontal pressure. Sharman also stated that there are 'eleven to thirteen body-rings' and described the eighth as having a long spine. Two of Sharman's specimens (Pl. 52, figs. 6, 8) and one collected by the writer show complete holaspide thoraces with twelve segments and there is none with any other number. Of the fragmentary thoraces, none has more than seven segments anterior to the macropleural one or (with the exception of an abnormal specimen described below) other than four between it and the pygidium; the macropleural segment appears to be the eighth in every case and the thorax may be taken as normally having twelve segments. Sharman's comparison of the pygidium with that of *Olenus micrurus* Salter was apposite at that time; in 1908, however, Lake (p. 56, pl. 5, fig. 12) showed that the pygidium of the latter species has a small pair of marginal spines, whereas that of *I. nuneatonensis* has not.

The somewhat unusual shape of the thorax of *I. nuneatonensis* recalls that of *Leptoplastus abnormis* Westergård (1944) and to some extent that of *Centroleura* as described by Öpik (1961), who considered it supported his idea that *Centroleura* was a 'pelagic hunter'. *Irvingella* may have had a similar mode of life.

Abnormal development. Palmer (1965, pl. 6, fig. 11) illustrated an asymmetrical pygidium of *Irvingella major*; three examples of asymmetrical development have been noted in *I. nuneatonensis*, in every case affecting the posterior part of the exoskeleton. In the specimen illustrated on Plate 52, fig. 6 (GSM 50283), the axial ring and right-hand pleura of the last (twelfth) thoracic segment are free but the left pleura is fused with the

pygidium. This type of deformity has been illustrated in species of *Paradoxides* by Westergård (1936, pl. 8, fig. 4, and pl. 10). The pygidium of GSM JR3127, shown in Plate 52, fig. 11, and text-fig. 2a, has the second axial ring incompletely developed on one side (compare the occipital ring of *Rossaspis superciliosa* (Ross) illustrated in Harrington *et al.* 1959, fig. 82c, p. O110). It may be that the right-hand pleural part of this segment was not developed at all and that it is for this reason that the right pleural region of the pygidium is smaller than the left.



TEXT-FIG. 2. (a) Deformed pygidium of the specimen shown in Plate 52, fig. 11, GSM JR3127; (b) Deformed pleurae and pygidium, GSM JR3139. Both $\times 10$.

The anterior part of the fragmentary thorax and pygidium (GSM JR3139) shown in text-fig. 2b is, so far as can be seen, quite normal, including the macropleural segment and the one posterior to it; the latter two segments are accordingly taken to be the eighth and ninth, as usual. The tenth segment presents the normal appearance along its anterior margin but the posterior margin is oblique to the sagittal line, the pleura being abnormally swollen behind the spine and the ring apparently longer on the right than on the left. The eleventh and final free thoracic segment is also oblique to the sagittal line and has an unusually short pleural spine. The anterior margin of what appears to be the pygidium is oblique and it seems that either the first or second of the four axial rings seen on the fragment preserved is imperfectly developed in a manner somewhat similar to the second axial ring of the pygidium shown in text-fig. 2a.

Although the specimen appears to have had only eleven free thoracic segments it is too large for this to be ascribed to immaturity, and it seems likely that the abnormalities in form and in number of the posterior thoracic segments are connected in some way. The right pleura attached to the tenth axial ring has the appearance of being composed of two ankylosed pleurae, presumably the tenth and eleventh; if so, the eleventh axial ring may also be fused with the tenth, and the segment corresponding to the twelfth in the normal thorax appears as the eleventh here. Alternatively, if the swelling on the tenth pleura is a pathological growth, it may be surmised that this displaced or distorted the eleventh segment somewhat and caused the right-hand pleura of the twelfth segment

to be suppressed altogether; in this case it would appear that the twelfth axial ring is fused with the pygidium.

Comparison with other species. *Irvingella nuneatonensis* is distinguished from the group of species separated by some authors as 'Parairvingella' [*I. angustilimbata* Kobayashi, *I. convexa* (Kobayashi, not Ivshin), *I. megalops* (Kobayashi), *I. specioza* (Ivshin) and *I. tropica* Öpik] by the absence of a distinct anterior border and border-furrow in cranidia of mature specimens (more than 2.0 or 2.5 mm. long).

In *Irvingella major* Ulrich and Resser (see Palmer 1965, p. 48, pl. 6, figs. 9–15) the glabella is cylindrical and with a rounded front, not tapered and truncate anteriorly as in *I. nuneatonensis*, and it is more convex transversely; the eyes are longer with their anterior ends closer together, and (in large cranidia only) the interocular cheeks are narrower than half the glabellar width, not wider as in *I. nuneatonensis*.

The glabella of *I. flolri* Resser (see Palmer 1965, p. 47, pl. 6, figs. 16, 19, 20, 24) is much like that of *I. nuneatonensis* except that in the former the S2 furrows are obscure and S3 absent; in large cranidia the interocular cheeks are narrower.

Irvingella transversa Palmer (1965, p. 48, pl. 6, figs. 7, 8) has wider interocular cheeks than *I. nuneatonensis*; the glabella is not tapered, the eyes are longer and their anterior ends are further apart.

The glabella of *I. suecica* Westergård (1947, p. 16, pl. 3, figs. 1–3, 5?, 6?, not fig. 4) is less convex longitudinally and has weaker S2 furrows than those of *I. nuneatonensis*, and S3 are absent; the anterior border persists to a later stage of growth and the anterior margin appears not to bend abruptly down as it does in *I. nuneatonensis* and other species of the genus.

I. nuneatonensis differs from *I. convexa* Ivshin (1962, p. 54; not *Komaspis* (*Parairvingella*) *convexa* Kobayashi) by having a tapered glabella with S3 furrows present and wider cheeks. It differs also from *I. kassini* Ivshin (1962, p. 56) in having a tapered glabella with S2 and S3 present. The tapered glabella with S3 impressed likewise serves to separate it from the species *I. platycephala* described by Rusconi (1953).

Horizon and localities. The type-material was collected in 1886 by J. Rhodes from within the upper 250 ft. of the Outwoods Shales in Stockingford Railway Cutting, 1,200 yards N. 54° E. of St. Paul's Church, Stockingford, west of Nuneaton, Warwickshire (NGR SP3429.9207 or thereabouts); precise horizon uncertain. A few specimens of *Irvingella*, provisionally referred to *I. nuneatonensis* but with the diagnostic features not preserved, were collected by the writer in 1963 from a shallow excavation about 110 yards east by south of the Lodge in Parkhill Outwoods and 30 yards north of the Atherstone–Coleshill road (B4116), one mile south-west of Atherstone, Warwickshire (NGR SP2980.9654); the shale fragments were not definitely *in situ* but nevertheless probably came from the top 100 ft. of the Outwoods Shales.

The horizon is high in the *Olenus* Zone, not lower than the subzone of *Olenus dentatus* and quite probably higher.

The evidence both for the stratigraphical and zonal horizon given above is somewhat circumstantial and as the stratigraphical palaeontology of the Outwoods Shales has not been published the main points are stated below.

Illing (1913, p. 453) subdivided the 'Middle Stockingford' or 'Oldbury Shales' of Lapworth (1898, pp. 345-6) as follows:

Oldbury Shales	{	Monks Park Shales
		Moor Wood Flags and Shales
		Outwoods Shales
		Abbey Shales

He published a map (Illing 1916, pl. 38) showing that the Outwoods Shales (which are somewhat over 1,000 ft. in thickness) crop out in Stockingford Railway Cutting. However, Mr. K. Taylor and I have noted fragments of the Moor Wood Flags at the extreme west end of this cutting. According to Lapworth (1898, pp. 346, 347) *Irvingella* [*Olenus*?] *nuneatonensis* was found at a somewhat higher horizon in Stockingford Cutting than '*Agnostus pisiformis* var. *sociale*' (= *Homagnostus obesus* Belt sp.); since I have collected the latter species from a few horizons in the cutting up to about 250 ft. stratigraphically below the base of the Moor Wood Flags, *I. nuneatonensis* was probably collected from this 250-ft. interval. As mentioned above, the specimens of *Irvingella* collected by the writer appear to have come from the upper 100 ft. of the Outwoods Shales.

The zonal arrangement applied to the early Upper Cambrian of north-west Europe is as follows (Westergård 1947, pp. 20, 21):

Zones	Subzones
<i>Parabolina spinulosa</i> with <i>Orusia lenticularis</i>	{ <i>P. spinulosa</i> <i>P. brevispina</i>
<i>Olenus</i> with <i>Homagnostus obesus</i>	{ <i>O. scanicus</i> with ' <i>Polyphyma</i> ' <i>angelini</i> <i>O. dentatus</i> <i>O. attenuatus</i> <i>O. wahlenbergi</i> <i>O. truncatus</i> } with <i>Glyptagnostus reticulatus</i> <i>O. gibbosus</i> } <i>reticulatus</i>
<i>Agnostus pisiformis</i>	—

I have detected the Subzones of *O. gibbosus*, *O. truncatus* and *O. wahlenbergi* in the Outwoods Shales and have found that the last of these is overlain at a horizon some 400 ft. below the base of the Moor Wood Flags by *Olenus cataractes* Salter accompanied by *Proceratopyge tullbergi* Westergård; the latter species is recorded by Westergård from the upper part of the Subzone of *O. dentatus* and by Tullberg from the Subzone of *Protopeltura aciculata* (= *Parabolina brevispina*; see Westergård 1947, p. 12). *I. nuneatonensis* occurs at a substantially higher horizon than that with *P. tullbergi* and *O. cataractes*, and is accordingly thought to be either above the Subzone of *O. dentatus* or possibly within its upper part.

The Moor Wood Flags have yielded no fossils, but in the Geological Survey Merevale No. 1 Borehole the lower beds of the overlying Monks Park Shales were found to contain *Parabolina* cf. *brevispina* Westergård, with *P. spinulosa* (Wahlenberg) at a somewhat higher horizon, both species being associated with abundant specimens of *Orusia lenticularis* (Wahlenberg). *I. nuneatonensis* thus appears to occur below the Subzone of *P. brevispina*. This conclusion is not in conflict with the situation in Sweden for although Westergård (1947, p. 17) originally considered that *I. suecica* possibly came from a

horizon near the base of the *Peltura* Zones he was later able to show that a subzone below that of *Parabolina spinulosa* was more probable (Westergård 1949, p. 606).

Correlation. In North America, assemblages of trilobite genera are used to define the standard Cambrian zones, each of which is named after one of the included genera. The zones of the Upper Cambrian are as follows:

Zones	Stages
Saukia	Trempealeuan
Ptychaspis and Prosaukia	Franconian
Conaspis	
Elvinia	
Dunderbergia	Dresbachian
Aphelaspis	
Crepicephalus	
Cedaria	

Generally speaking there are so few genera of trilobites known from both Europe and the mid-continent regions of North America that correlation between the respective series of standard zones is quite uncertain. Palmer, however, has used the subspecies *Glyptagnostus reticulatus reticulatus* to correlate the lower part of the *Aphelaspis* Zone with the lower subzones of the *Olenus* Zone (Palmer 1962, text-fig. 9, p. 10). In his research on the trilobites from the Great Basin Region in the United States, Palmer (1965, text-fig. 15) showed that *Irvingella* first appears slightly above the base of the *Elvinia* Zone, having evolved from *Elviniella laevis* Palmer. He also showed that the successive species of *Irvingella* lose the distinct anterior border at successively earlier stages in ontogeny; thus *I. angustilimbata*, the only species to retain the anterior border in fully grown individuals, is confined to the lower part of the *Elvinia* Zone, and the other species (*I. major*, *I. ffolhri*, and *I. transversa*) appear only in the upper part. *I. nuneatonensis* is most similar to the species *I. major* and *I. ffolhri*, and probably developed directly or indirectly from *I. angustilimbata*; if so, it is certainly no older than *I. angustilimbata* and is probably of the same age as the species in the upper part of the *Elvinia* Zone, or a little younger. This suggests that the top of the *Elvinia* Zone is no higher than the top of the *Olenus* Zone, that is, somewhat lower than the position tentatively suggested by Palmer in his correlation table (1962, text-fig. 9, p. 10).

Acknowledgements. I am grateful to Dr. A. R. Palmer for casts of North American species of *Irvingella* and for interesting discussion; Professor O. M. B. Bulman, for discussion of the deformed specimen shown in text-fig. 2b; Mr. J. D. D. Smith for the loan of specimens in the collection of the Geological Survey and Museum; Mr. K. Taylor for discussion of the stratigraphy of the Stockingford Shales; and the late Sir William Dugdale, Bart., for permission to excavate for *Irvingella nuneatonensis* on his land. This study was initiated at the suggestion of Sir James Stubblefield, to whom I am indebted for various suggestions and advice, and was mostly carried out at the Sedgwick Museum, Cambridge, during the tenure of a D.S.I.R. Studentship. This paper is published by permission of the Director, Institute of Geological Sciences.

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PALYNOLOGY OF THE SPRINGER FORMATION OF SOUTHERN OKLAHOMA, U.S.A.

by CHARLES J. FELIX and PATRICIA PARKS BURBRIDGE

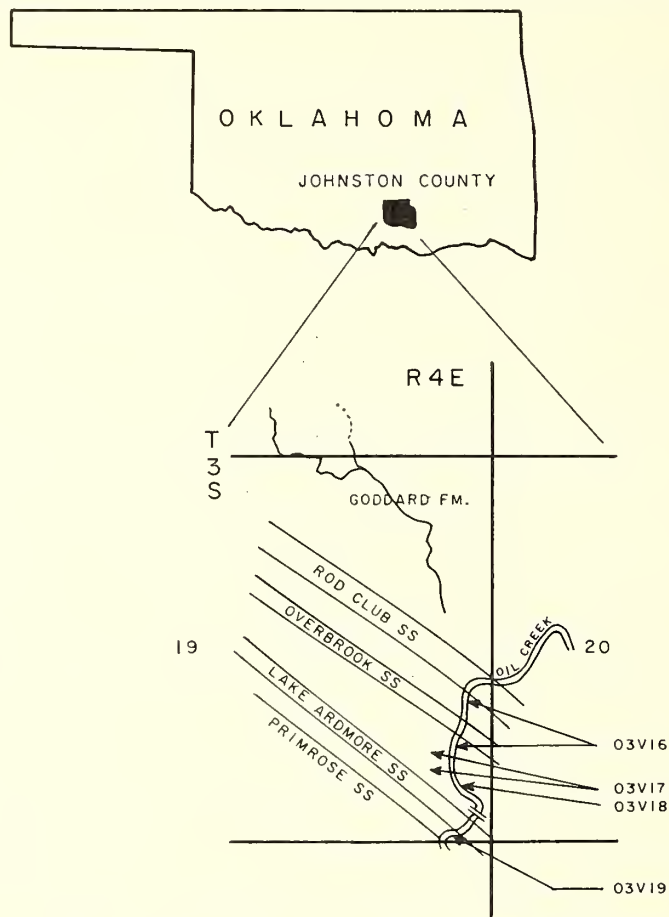
ABSTRACT. Twenty-three surface samples were studied from the Springer formation at its exposure in Johnston County, Oklahoma. The Springer formation is of interest because of the commercial occurrence of oil and gas in its subsurface sandstones, but there has been wide disagreement as to its correct age. The microflora is transitional in character with Mississippian and Pennsylvanian spores represented, and it is regarded as a transgressive facies from the Mississippian Goddard formation to the Pennsylvanian Morrow formation in the area studied. The systematic description of 104 microspore species is included in this paper. Seven new genera and thirty-five new species are proposed. One new name combination is suggested. The new genera represented are *Costatascyclus*, *Cystoptychus*, *Hadrohercos*, *Nexuosisporites*, *Tantillus*, *Trochospora*, and *Scutulum*. The remaining sixty-nine species are referable to previously described taxa and include representatives with ranges from Tournaisian to Westphalian B in terms of European nomenclature. By North American nomenclature the range would be from Kinderhook to Atokan.

THE Springer formation has long been of interest to students of geology, and this has been particularly true in the Ardmore Basin of Oklahoma where the structural instability during Pennsylvanian time has rendered correlations difficult. Each of the sandstones in the Springer contains oil and gas in commercial amounts in areas of southern Oklahoma. Tomlinson and McBee (1959) noted that these sands provided more than half of the new oil reserves discovered in Oklahoma during the 1941–55 period.

This study was originally initiated as a palynological project to determine the plant microfossil assemblages of the Goddard formation at its type section on the Goddard Ranch locality as described by Westheimer (1956) in Sections 18 and 19, T.3S, R.4E, Johnston County, Oklahoma. Inasmuch as the Caney and Springer formations are also well exposed at the Goddard Ranch locality, it was decided to determine whether a separation of the Caney, Goddard, and Springer formations could be made on spore assemblages. The Goddard and Caney phases of this study have been conducted by the Oklahoma Geological Survey under the direction of Dr. L. R. Wilson, and the Goddard formation palynology study is presently available in an unpublished graduate thesis (Wiggins 1962). The actual Goddard Shale exposure in the type section as defined by Westheimer (1956) has been inundated by construction of a reservoir, and Wiggins (1962) made his collections in Section 20 to the east of the flooded area. The surface Springer section treated in this study is considered to include three persistent sandstone members separated by shales (text-fig. 1). These are the Rod Club, Overbrook, and Lake Ardmore sandstones. The Rod Club is the basal unit immediately above the Goddard. The Overbrook sandstone was only $4\frac{1}{2}$ ft. thick at this exposure and was not mapped by Westheimer (1956).

There still exists considerable debate and much disagreement among palaeontologists and geologists as to the age and rank of the Springer. The wide disparity of opinion is demonstrated in its treatment by various workers. Moore *et al.* (1944) included the Springer in the Morrow Series. Dott (1941) assigned the upper Caney to the Springer formation and placed the Springer within the Morrow subseries. Bennison (1956)

was of the opinion that some of the Morrow sandstone of northwestern Oklahoma probably represents elements of both a Springer and Primose (Pennsylvanian) age. Tomlinson and McBee (1959) have presented an excellent survey of the various viewpoints held by other investigators regarding the age of the Springer. The Editorial Committee of 'Petroleum Geology of Southern Oklahoma' (Hicks *et al.* 1956) defined the Springer as of group rank and included within this definition both the Springer and



TEXT-FIG. 1. Locality map of the Springer collecting area.

Goddard formations. Tomlinson and McBee (1959) likewise defined the 'Springer Group' as including the Goddard formation and the 'Springeran Series'. These authors employed the term 'Springeran Series' in the same sense as did Elias (1956, pp. 70, 89-91), with its upper limit being the base of the Primrose sandstone and the base of the Rod Club sandstone as the lower limit. They excluded the underlying Goddard formation from their 'Springeran Series' on the basis of Elias' (1956) evidence of a Chester age for the Goddard. Peace (1965) has also given an excellent summary of the problems of Springer stratigraphy in which he presents a tentative correlation of Springer outcrops with subsurface units and correlation of locally named subsurface

Springer sandstones of the Anadarko Basin with those of the Ardmore Basin. However, he made no attempt to locate the Mississippian–Pennsylvanian boundary.

Though not the assigned type locality for the Springer, the Goddard Ranch material was chosen for our study because of its excellent exposures of Caney, Goddard, and Springer, thus providing sequential comparative assemblages. In addition, the spore assemblages were quantitatively good and preservation generally superb. The findings and conclusions presented here also incorporate results from other palynological investigations of this laboratory. These include a five-year unpublished study of the subsurface Morrow, Springer, and Chester formations from 48 cored wells in the Anadarko Basin of Texas and Oklahoma. A two-year investigation was made of the microflora from the Atoka, Morrow, and Mississippian in the Morrow type area of western Arkansas; these consisted of 145 collections from 29 localities in Madison, Newton, Searcy, Stone, and Washington counties, Arkansas. In addition to these two major efforts, a number of other areas of investigation have provided accessory information. These are noted throughout the manuscript when spores are encountered common to the Springer. Chief among these are shales and coals associated with fourteen major coals of the lower Pottsville in south-eastern Kentucky and south-western Virginia and shale of surface occurrences from the Johns Valley, Jackfork, and Stanley shales of Oklahoma. Eventual publication of all these data is hoped for and planned.

The samples were also examined by X-ray diffraction techniques to determine mineral constituents and to ascertain whether mineralogical variations existed. This was done in conjunction with studies conducted to attempt correlations from surface to subsurface and to afford accurate identification of the Springer formation from field to field. Two major facies were recognized. One was a low clay, dominantly sand facies and was noted in samples O3V16–1 and O3V19–1. The second facies was a montmorillonite, mixed-layer clay, and the remaining shale samples were of this type.

A total of twenty-three outcrop collections were made and catalogued under four laboratory maceration numbers. The samples were taken as closely as possible in 20 ft. channel samples in order to maintain maximum uniformity (text-fig. 2).

Locality data

Unit O3V16. NW. $\frac{1}{4}$ NE. $\frac{1}{4}$ SE. $\frac{1}{4}$ Sec. 19, T.3S, R.4E. Johnston County, Oklahoma. Fourteen samples collected in an interval of 287½ ft. Lithology dark grey to buff, laminated shale. Sample no. 1 in the interval is a ‘grit’ marking the top of the Rod Club sandstone. *Sigillaria* remains were common in the grit.

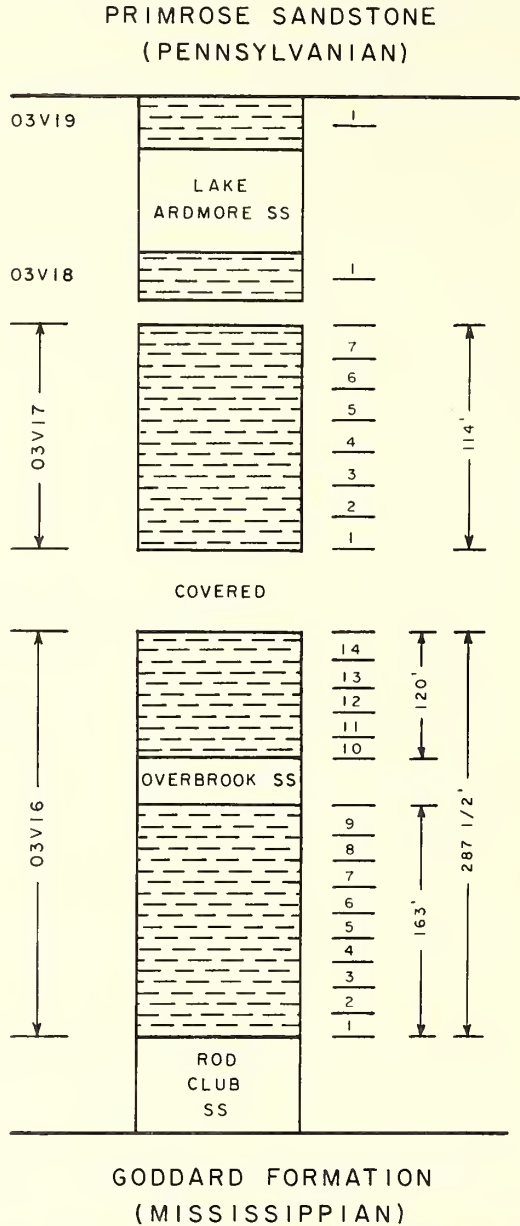
Unit O3V17. SW. $\frac{1}{4}$ SE. $\frac{1}{4}$ SE. $\frac{1}{4}$ NW. $\frac{1}{4}$ Sec. 19, T.3S, R.4E. Johnston County, Oklahoma. Seven samples collected in an interval of 114 ft. Lithology dark grey to buff, soft clayey shale.

Unit O3V18. SE. $\frac{1}{4}$ SW. $\frac{1}{4}$ SE. $\frac{1}{4}$ NW. $\frac{1}{4}$ Sec. 19, T.3S, R.4E. Johnston County, Oklahoma. Single sample collected on east bank of small, meander cut, 50 ft. below the Lake Ardmore sandstone outcrop. Lithology buff, soft, clayey shale.

Unit O3V19. NW. $\frac{1}{4}$ NW. $\frac{1}{4}$ NE. $\frac{1}{4}$ SW. $\frac{1}{4}$ Sec. 19, T.3S, R.4E. Johnston County, Oklahoma. Single sample collected immediately above the Lake Ardmore sandstone in wind gap gulley dissecting the massive Lake Ardmore sandstone. Lithology buff sandstone with dark, shale streaks.

Maceration techniques. No special problems were experienced in maceration of the Springer shales, and routine laboratory techniques were followed as described by numerous workers, especially Playford (1962, p. 570). Initial treatment consisted of hydrochloric acid, followed by hydrofluoric to digest mineral matter. Oxidation of

humic matter was accomplished with Schulze's solution, followed by alkali treatment when required. In some instances ultrasonic generation was effectively utilized. Final



TEXT-FIG. 2. Stratigraphic column of the Springer formation, showing position of sample collections.

separation was achieved with a zinc chloride flotation technique. Clearcol was the permanent mountant used and storage of residues was in Cellosolve.

Classification. The classification system of Potonié and Kremp (1954) is utilized, along with the subsequent treatments by the same authors (Potonié and Kremp 1955, 1956a, 1956b).

Acknowledgements. The authors wish to acknowledge their indebtedness to Dr. L. R. Wilson of the Oklahoma Geological Survey for graciously withdrawing his staff from the Springer area of study when it became evident that concurrent studies were being undertaken and for his useful assistance and encouragement in this problem and others through the years; to the Arkansas Geological Survey for its very helpful contribution of personnel and other assistance during the Morrow collecting project; to Mr. Virgil Wiggins of the Standard Oil Co. of California, who assisted in collecting the Goddard Ranch samples while a member of the Sun Oil Co. palynology staff, for the use of his unpublished data on the Caney and Goddard formations. Mr. Wiggins also provided comparative material of the sub-surface Chainman formation, Mississippian, for which he received the best paper award, west coast AAPG-SEPM, 1960. We are also indebted for comparative reference samples to Mr. M. S. Barss for samples of the Horton coal, to Dr. Geoffrey Playford for Visean and Tournaisian samples of his Spitzbergen material, and Dr. Roger Neves for samples of the material used in his 1958 and 1961 investigations of the Namurian. Thanks are also due to Dr. Russel A. Peppers of the Illinois Geological Survey for the loan of isotype slides from Kosanke's 1950 studies; to Dr. Samine Artüz for her advice and assistance at various times during the course of this work; and to Dr. Herbert Sullivan of the Pan American Petroleum Corporation, who has provided reference material from his several Visean and Tournaisian studies and who has given most generously of his time and advice. We are especially grateful to the Sun Oil Company for granting permission to publish and for financial assistance with illustration costs.

Anteturma SPORONITES (R. Potonié) Ibrahim 1933

Genus CHAETOSPHAERITES Felix 1894

Type species. *C. bilychnis* Felix 1894.

Chaetosphaerites pollenisimilis (Horst) Butterworth and Williams 1958

Plate 53, figs. 1, 2

1955 *Sporonites pollenisimilis* Horst, pp. 150–1, pl. 24, figs. 84–87.

1957 *Sporonites cylindricus* (Horst) Dybová and Jachowicz, pp. 56–57, pl. 1, figs. 1–4.

1958 *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams, p. 359, pl. 1, figs. 1–3.

1962 *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams; Playford, p. 573, pl. 78, figs. 1–2.

Description. Most of the specimens encountered in the Springer were the bicellular type, which seems to be the usual form. However, three-celled specimens were also common.

Dimensions. (20 specimens.) Diameters range from $14 \times 27 \mu$ to $16 \times 30 \mu$.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Anteturma SPORITES H. Potonié 1893

Turma TRILETES (Reinsch) Potonié and Kremp 1954

Subturma AZONOTRILETES Luber 1935

Infraturma LAEVIGATI (Bennie and Kidston) Potonié and Kremp 1954

Genus LEIOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *L. sphaerotriangulus* (Loose) Potonié and Kremp 1954.

Leiotriletes ornatus Ischenko 1956

Plate 53, fig. 3

1956 *Leiotriletes ornatus* Ischenko, p. 22, pl. 2, figs. 18–21.

1960 Spore type 1 of Love, p. 122, pl. 2, fig. 9, text-fig. 12.

1962 *Leiotriletes ornatus* Ischenko; Playford, p. 575, pl. 78, figs. 7–8.

Description. Radial, trilete; subtriangular with sides slightly convex. Laesurae distinct, straight, extending to margins; prominent raised lips 2–3 μ wide. Exine 2–3 μ thick, laevigate.

Dimensions. (10 specimens.) Equatorial diameter 30–42 μ .

Leiotriletes subintortus (Waltz) Ischenko 1952 var. *rotundatus* Waltz 1941

Plate 53, figs. 4, 5

1941 *Azonotriletes subintortus* Waltz var. *rotundatus* Waltz in Luber and Waltz, pp. 13–14, pl. 2, fig. 15b.

EXPLANATION OF PLATE 53

All figures $\times 500$ unless otherwise indicated.

Figs. 1, 2. *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams 1958. 1, Slide O3V16–4 (R-1), location 53.5 $\times$ 120.7 (Ref. 32.3 $\times$ 118.7). 2, Slide O3V16–4 (R-2), location 37.5 $\times$ 123.2 (Ref. 34 $\times$ 118).

Fig. 3. *Leiotriletes ornatus* Ischenko 1956. Proximal surface; Slide O3V16–11 (6), location 29 $\times$ 110.2 (Ref. 31.7 $\times$ 116.9).

Figs. 4, 5. *Leiotriletes subintortus* (Waltz) Ischenko 1952 var. *rotundatus* Waltz 1941. 4, Proximal surface; Slide O3V16–4 (R-1), location 52 $\times$ 117.5 (Ref. 32.3 $\times$ 118.7). 5, Proximal surface; Slide O3V16–3 (6), location 28.9 $\times$ 116.1 (Ref. 33 $\times$ 117.9).

Figs. 6, 7. *Leiotriletes tumidus* Butterworth and Williams 1958. 6, Proximal surface; Slide O3V16–13 (A-1), location 9.5 $\times$ 122.5 (Ref. 31.1 $\times$ 117.9). 7, Proximal surface; Slide O3V16–13 (A-2), location 19.1 $\times$ 111.5 (Ref. 32.2 $\times$ 117.9).

Fig. 8. *Punctatisporites divaricatus* sp. nov. Holotype. Proximal surface; Slide O3V16–14 (5), location 13 $\times$ 124 (Ref. 32.3 $\times$ 117.6).

Fig. 9. *Punctatisporites flexuosus* sp. nov. Holotype. Proximal surface; Slide O3V16–11 (1), location 45.5 $\times$ 119.8 (Ref. 32 $\times$ 118.7).

Figs. 10, 11. *Punctatisporites heterofiliferus* sp. nov. 10, Holotype. Proximal surface; Slide O3V16–3 (6), location 10.2 $\times$ 124 (Ref. 33 $\times$ 117.9). 11, Trilete split to form triangular opening; Slide O3V16–3 (5), location 54.9 $\times$ 115.6 (Ref. 33.7 $\times$ 118).

Fig. 12. *Punctatisporites incomptus* sp. nov. Holotype. Proximal surface; Slide O3V16–11 (5), location 38 $\times$ 110.8 (Ref. 32.6 $\times$ 117.8).

Fig. 13. *Punctatisporites irrasus* Hacquebard 1957. Proximal surface; Slide O3V16–14 (5), location 43.2 $\times$ 113.2 (Ref. 32.3 $\times$ 117.6).

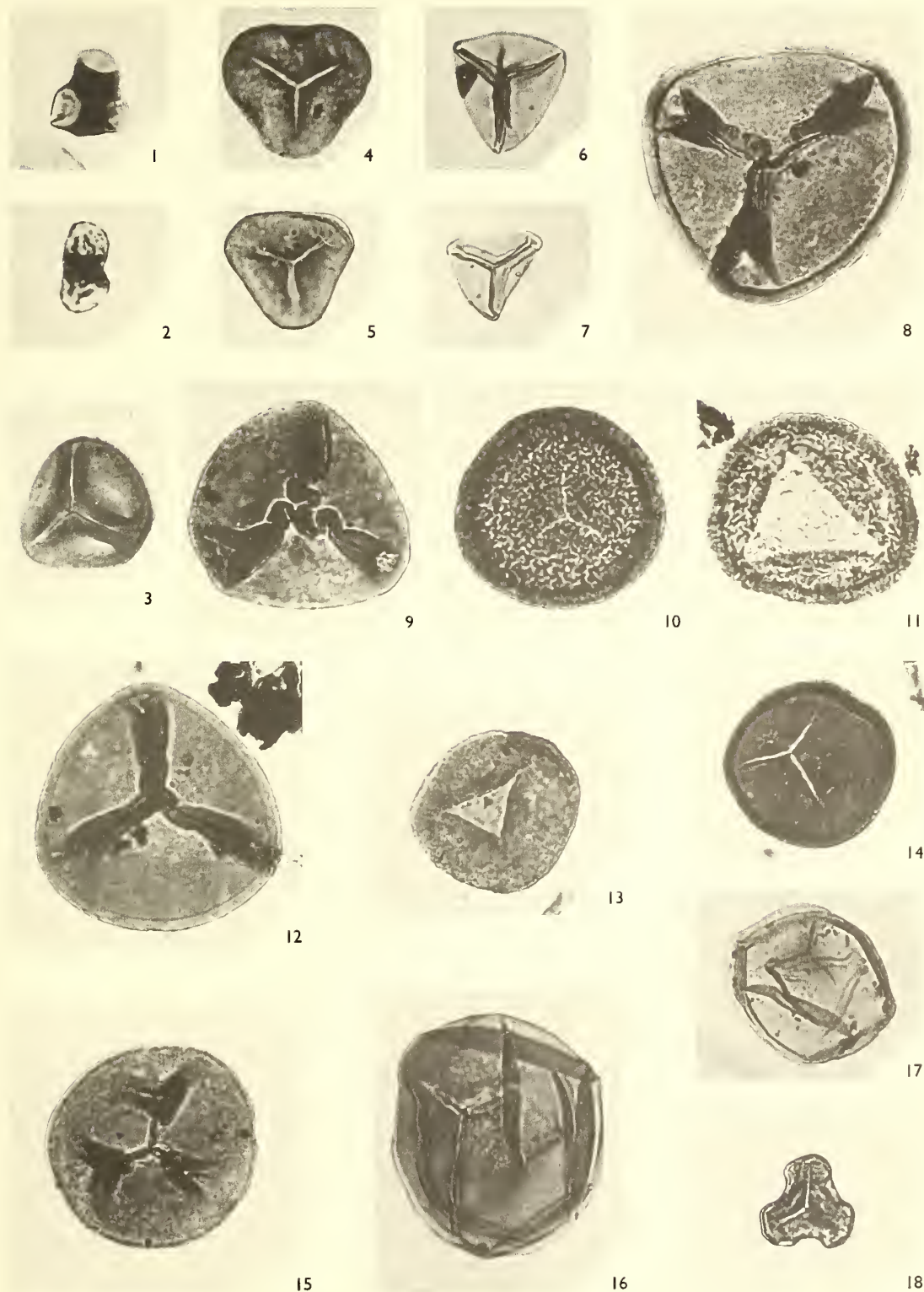
Fig. 14. *Punctatisporites solidus* Hacquebard 1957. Proximal surface; Slide O3V16–9 (5), location 18.9 $\times$ 107.8 (Ref. 32.4 $\times$ 118.6).

Fig. 15. *Punctatisporites trifidus* sp. nov. Holotype. Proximal surface; Slide O3V16–3 (5), location 38.5 $\times$ 127.5 (Ref. 33.7 $\times$ 118).

Fig. 16. *Calamospora* cf. *hartungiana* Schopf 1944. Proximal surface; Slide O3V17–2 (1), location 12 $\times$ 125.6 (Ref. 31 $\times$ 117.9).

Fig. 17. *Calamospora* cf. *parva* Guennel 1958. Proximal surface; Slide O3V16–11 (1), location 54.5 $\times$ 120.5 (Ref. 32 $\times$ 118.7).

Fig. 18. *Waltzispota sagittata* Playford 1962. Proximal surface; Slide O3V16–3 (6), location 23 $\times$ 110 (Ref. 33 $\times$ 117.9).



1952 *Leiotriletes subintortus* (Waltz) Ischenko var. *rotundatus* Waltz; Ischenko, p. 11, pl. 1, fig. 7.

1962 *Leiotriletes subintortus* (Waltz) Ischenko var. *rotundatus* Waltz; Playford, pp. 574–5, pl. 78, figs. 5–6.

Description. Radial, trilete, subtriangular with rounded apices and concave sides. Laesurae distinct, extending nearly to spore margin. Exine 1–2 μ thick. Laevigate.

Dimensions. (25 specimens.) Equatorial diameter 30–45 μ .

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Leiotriletes tumidus Butterworth and Williams 1958

Plate 53, figs. 6, 7

Description. Radial, trilete, subtriangular with sides convex to slightly straight. Laesurae distinct, straight, extending nearly to body margin, lips prominent. Body wall thin, approximately 1 μ thick, laevigate.

Dimensions. (25 specimens.) Equatorial diameter 30–45 μ .

Discussion. The Springer specimens do not show the proximal tumidity with the degree of regularity noted by Butterworth and Williams (1958). However, this feature is evident on some specimens, and any further specific separation seems inadvisable.

Genus PUNCTATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *P. punctatus* Ibrahim 1933.

Punctatisporites divaricatus sp. nov.

Plate 53, fig. 8

Diagnosis. Radial, trilete, subtriangular. Laesurae slightly sinuous, equal to two-thirds to four-fifths of radius; prominent lips increase in width toward terminal ends, range in width from 2–5 μ at junction area to 5–10 μ terminally; commissure distinct and suture bifurcating terminally with each division 5–10 μ long; lips flare out sharply on either side of suture division. Exine 3–5 μ thick and always well defined, essentially laevigate but sometimes minutely punctate.

Dimensions. (25 specimens.) Equatorial diameter 60–95 μ (average 70–85 μ).

Holotype. Slide O3V16–14 (5). Location 13 $\times$ 124 (Ref. 32 $\times$ 117.6).

Description. Holotype subtriangular, diameter 80 $\times$ 85 μ ; laesurae slightly sinuous, 26–35 μ in length, four-fifths of spore radius; prominent lips 5 μ wide at junction with rays to 10 μ wide at terminal ends; commissure distinct, ending in divisions of 15 μ in length; exine 5 μ thick, minutely punctate when viewed at high magnification.

Comparison. The conspicuous wall serves to distinguish it from *P. flexuosus*, along with the less sinuous laesurae. It differs from *P. incomptus* by the widely expanded and more sinuous lips, as well as the more pronounced thickened exine.

Punctatisporites flexuosus sp. nov.

Plate 53, fig. 9

Diagnosis. Radial, trilete, subtriangular. Laesurae sinuous to convolute, equal to four-fifths of radius, frequently extending to margin; prominent lips increase in width towards terminal ends, ranging in width from $2\text{--}3.5\ \mu$ wide at junction area to $5\ \mu$ in width terminally; commissure distinct and bifurcating terminally with each division $5\text{--}7.5\ \mu$ long; lips expand sharply on either side of suture divisions. Exine indistinct but measurable walls $3.5\text{--}5\ \mu$ thick recorded. Body laevigate.

Dimensions. (25 specimens.) Equatorial diameter $55\text{--}80\ \mu$ (average $60\text{--}75\ \mu$).

Holotype. Slide O3V16-11 (1). Location 45.5×119.8 (Ref. 32×118.7).

Description. Holotype subtriangular, diameter $65 \times 69\ \mu$; laesurae markedly convolute in area of junction of rays, $30\ \mu$ in length and equal to over four-fifths of radius; lips $3.5\ \mu$ wide in area of convolutions to $5\ \mu$ wide at terminal ends; wall not sharply defined but $5\ \mu$ in thickness.

Discussion. In several specimens, including the holotype, the commissure was noted to be sinuous also and often followed the twistings of the lips. This indicated that the lips and commissure are not features of different exine structures as was suggested for *P. validus*.

Comparison. The excessive convolutions of the laesurae serve to differentiate the species from *P. incomptus* and *P. divaricatus*, while its rather indistinct exine also differs from the well-defined exine of these two species.

Punctatisporites heterofiliferus sp. nov.

Plate 53, figs. 10, 11

Diagnosis. Radial, trilete, circular. Laesurae well-defined, simple, straight, sometimes indistinct due to ornamentation, extending nearly to body margin, no lip development; trilete frequently split to form a triangular-shaped opening (Pl. 53, fig. 11) ranging from $20 \times 20\ \mu$ to $40 \times 45\ \mu$ over-all. Wall thick, $5\text{--}7\ \mu$. Sculpture finely obervermiculate, composed of short, thread-like markings, often branching but never anastomosing to form a reticulum.

Dimensions. (25 specimens.) Equatorial diameter $48\text{--}68\ \mu$ (average $55\text{--}65\ \mu$).

Holotype. Slide O3V16-3 (6). Location 10.2×124 (Ref. 33×117.9).

Description. Holotype circular, $63.5 \times 66\ \mu$; laesurae straight, simple, $25\ \mu$ long and extending nearly to the margin; wall distinct, $6\ \mu$ thick. Sculpture minutely obervermiculate, branching slightly, but not reticulate.

Comparison. *P. vermiculatus* Kosanke 1950 (p. 19, pl. 2, fig. 4) is similar, but in addition to the lengthy geological time gap existing, Kosanke's species is described as having a poorly defined trilete and is deeply incised by a well-developed vermiculate sculpture.

The minor sculpture of *P. parviverruculatus* Playford 1962 (p. 577, pl. 78, fig. 14) is quite similar to that of *P. heterofiliferus*. However, Playford's species has a much thinner exine and is subject to folding. The exine sculpture is also less well defined, since he noted that oil immersion is frequently necessary in studying. The infravermiculate sculpture also differs from *P. heterofiliferus*, which has the vermiform markings definitely positioned upon the exine. The degree of sculpture of *P. heterofiliferus* appears to lie between that for *P. verruculatus* and *P. parviverruculatus*. The triangularly split trilete probably does not occur more than 50 per cent. of the time and should not be considered as diagnostic. However, it is frequent enough to warrant attention.

Punctatisporites incomptus sp. nov.

Plate 53, fig. 12

Diagnosis. Radial, trilete, subtriangular. Laesurae straight except for slight undulation of lips, equal to three-fourths to four-fifths of radius; prominent raised lips increase in width towards outer limits, range from 2.5–4.5 μ in width at junction point to 4–6.5 μ terminally; commissure distinct and suture has slight terminal bifurcation, with each division about 5 μ in length, lips tending to flare out noticeably on each side of divided suture, with sutures slightly exceeding the lips in over-all length. Wall distinct, 3–5 μ thick, laevigate.

Dimensions. (25 specimens.) Equatorial diameter 60–90 μ (average 65–80 μ).

Holotype. Slide O3V16–11 (5). Location 38 $\times$ 110.8 (Ref. 32.6 $\times$ 117.8).

Description. Holotype subtriangular, diameter 74 $\times$ 77 μ ; laesurae straight, 30–35 μ in length, four-fifths of spore radius; prominent lips from 3.5 μ wide at junction with rays at apex to 6.5 μ wide at terminal ends; commissure distinct, ending in divisions of 5 μ in length; exine 4 μ thick, laevigate.

Comparison. This species is distinguished from *P. validus* by the more pronounced exine, undulation of the lips, and the regular bifurcation of the rays and accompanying expansion of the lips. The lips do not display the prominent height of those in *P. validus*. It may be distinguished from *P. divaricatus* and *P. flexuosus* by differences in exine thickness and a less conspicuous expansion of the rays.

Punctatisporites irrasus Hacquebard 1957

Plate 53, fig. 13

Description. Radial, trilete, circular to oval. Laesurae distinct, simple, straight, one-half to three-quarters of spore radius; germinal sutures commonly gaped open to form triangular opening with darker intertectal area. Body wall distinct, 2–3 μ thick, laevigate to minutely granulose.

Dimensions. (25 specimens.) Equatorial diameter 48–75 μ .

Discussion. There is the possibility that *Leiotriletes microtriangulus* Artüz 1957 is the same, but assignment cannot be definite without reference to Artüz's material.

Hacquebard's (1957) West Gore assemblage was available for comparison, as well as Sullivan's (1964a) Plump Hill and Puddlebrook material, and the Springer specimens are indistinguishable from *P. irrasus*. However, it never attained the high percentages recorded by Hacquebard and by Sullivan, where the species composed one-fourth to one-third of the total assemblages. The highest occurrence recorded was in O3V17-5 where it totalled 11 per cent.

Punctatisporites solidus Hacquebard 1957

Plate 53, fig. 14

Description. Radial, trilete, circular to subcircular in outline. Laesurae distinct, simple, straight, length four-fifths spore body radius. Body laevigate. Wall 3-4 μ thick.

Dimensions. (15 specimens.) Equatorial diameter 36-60 μ .

Punctatisporites trifidus sp. nov.

Plate 53, fig. 15

Diagnosis. Radial, trilete, circular. Laesurae straight, equal to one-half to two-thirds of radius; rays bifurcating at their termini with each division frequently continuing a distance equal to their length before division; prominent, highly elevated lip structures originate on either side of suture about one-half the distance from the ray's point of junction to the terminal point of division; lips flare out, accompanying the suture bifurcation on either side. Exine thin, 1.5-2.5 μ thick, laevigate.

Dimensions. (25 specimens.) Equatorial diameter 50-75 μ .

Holotype. Slide O3V16-3 (5). Location 38.5 $\times$ 127.5 (Ref. 33.7 $\times$ 118).

Description. Holotype circular, diameter 62.5 $\times$ 65 μ ; laesurae straight, 17-22 μ in length, equal to two-thirds distance of radius; sutures bifurcate about two-thirds their length with divisions accompanied by prominent lips about 5 μ in width; exine 2 μ thick, laevigate.

Discussion. The rays are often accompanied their entire length by slightly developed labial structures, but these are usually very difficult to discern and the prominence of the conspicuous terminal lips serves to overshadow any other features. The divided suture and widely flared lips are reminiscent of the upper Pennsylvanian genus *Cadiospora* but does not reveal any tendency to continue as arcuate thickenings as in *Cadiospora* and various megaspore genera.

Comparison. *Leiotriletes auritus* Ischenko 1956 is probably the same, but again the brevity of description and illustration prevent making an accurate comparison.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Punctatisporites validus sp. nov.

Plate 54, figs. 1, 2

Diagnosis. Radial, trilete, subcircular. Laesurae distinct, straight, equal to over four-fifths of radius, frequently extending to spore margin; prominent raised lips individually $3-5\ \mu$ wide and commissure distinct; rays commonly not bifurcated, but in rare instances a slight terminal division is present. Exine $2-3\ \mu$ thick, laevigate, body occasionally with one or two minor folds. Spores generally retaining tetrad grouping.

Dimensions. (50 specimens.) Equatorial diameter $60-94\ \mu$ (average $70-80\ \mu$).

Holotype. Slide O3V16-11 (5). Location 15.5×123.1 (Ref. 32.6×117.8).

Description. Holotype subcircular, diameter $86\ \mu$; laesurae straight, $40\ \mu$ long, extending nearly to spore margin, prominent lips $4.5\ \mu$ wide, commissure visible; exine $2.5\ \mu$ thick, laevigate.

Discussion. A feature commonly observed in this spore is the difference in length of the actual sutural opening and the lips, as well as the fact that they do not always overlies each other. Staplin and Jansonius (1964) have noted this in their densospore study and regarded the laesura as a structure of the intexine and the sutural ridge to be an exoexine structure. The tetrad character is considered of diagnostic significance since the tetrad grouping appeared to be retained in most instances, even through the maceration process. This feature does serve to increase the difficulty of identification since the laesurae configuration is more or less obscured. The laesurae are one of the more reliable identification features. The prominent lips do not bifurcate as in *P. incomptus* or *P. trifidus*, and they maintain a constant dimension throughout their lengths. The straight laesurae with conspicuous raised lips are also characteristic of the species. Although there is an occasional slight terminal bifurcation of a suture, it is never to the degree noted in the other species of the genus described here and is never accompanied by the pronounced expansion of the lips. The wall is not as distinct as in *P. incomptus* or *P. divaricatus*. It is also the only spore of this group of *Punctatisporites* displaying a tendency, though slight, to folding and plication of the spore wall.

Comparison. *Trachytriletes auritus* Ischenko 1956 may well be the same. However, Ischenko described the ornamentation in the Russian spore as shagreen to tubercular. The brevity of the description and inadequacy of illustrations prevents any accurate comparison.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Genus CALAMOSPORA Schopf, Wilson, and Bentall 1944

Type species. *C. hartungiana* Schopf in Schopf, Wilson, and Bentall 1944.

Calamospora cf. *hartungiana* Schopf 1944

Plate 53, fig. 16

Description. Radial, trilete, originally spherical, compressed in lenticular outline with

numerous folds. Laesurae one-fourth to one-half radius, very thin lip development. Spore coat laevigate, 1–2 μ thick.

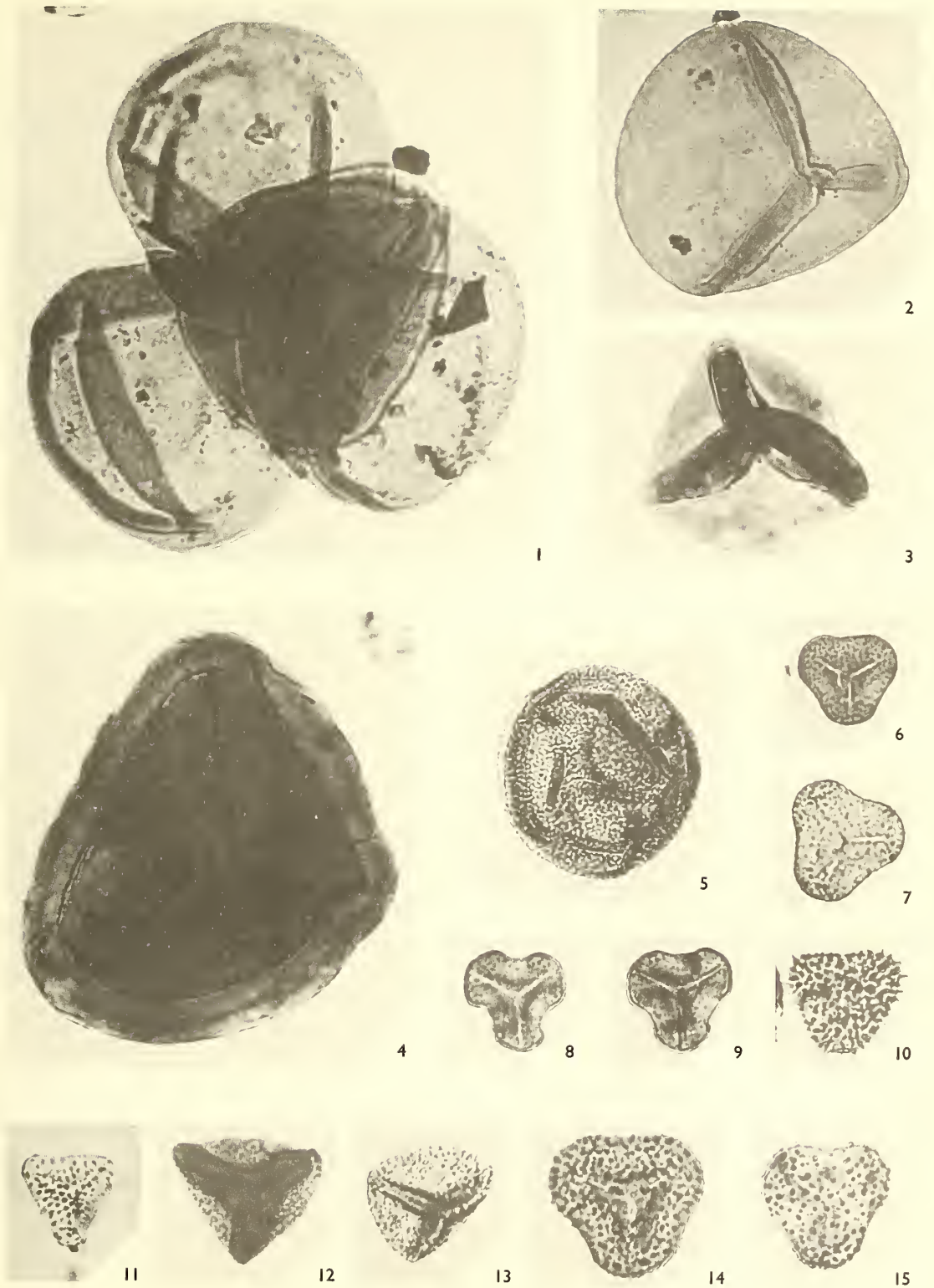
Dimensions. (50 specimens.) Equatorial diameter 45–100 μ (average 50–70 μ).

Discussion. *Calamospora* is very numerous in the Springer formation. However, the taxonomy of this taxon is still so poorly defined as to render definite segregation of species nearly impossible. The Springer specimens are within the size ranges of *C. breviradiata* Kosanke, characterized by short rays and an *area contagionis*, and of *C. liquida* Kosanke, with long rays and the *area contagionis* not present. *C. microrugosa* (Ibrahim) Schopf, Wilson, and Bentall 1944 is very similar to the Springer material and differs from *C. hartungiana* primarily in the lack of the *area contagionis*. These features appear useless diagnostically in view of the present assemblage. Specimens in all phases of the size range have been observed with long rays, with short rays, with and without the *area contagionis*. They could possibly be included in *C. microrugosa*, *C. liquida*, *C. exigua*, or *C. breviradiata*. However, every conceivable combination of diagnostic characters appears to exist in the Springer assemblage and no clearcut division seems possible. Hartung (1933) described degenerate spores from *Macrostachya* cones which fall within the size ranges of the Springer specimens and possess the *area contagionis*. However, he also observed mature spores of larger dimensions and without the *area contagionis* in the same cones. Such morphological development appears to be a factor in the heterogeneity of this Springer taxon.

EXPLANATION OF PLATE 54

All figures $\times 500$ unless otherwise indicated.

- Figs. 1, 2. *Punctatisporites validus* sp. nov. 1, Tetrad; Slide O3V16–11 (2), location 33 $\times$ 126 (Ref. 32 $\times$ 118). 2, Holotype. Proximal surface; Slide O3V16–11 (5), location 15.5 $\times$ 123.1 (Ref. 32.6 $\times$ 117.8).
 Fig. 3. *Gulisporites incomptus* sp. nov. Holotype. Proximal surface; Slide O3V16–9 (A-1), location 27.9 $\times$ 119 (Ref. 31 $\times$ 116.5).
 Fig. 4. Undescribed spore. Proximal surface; Slide O3V16–10 (2), location 39 $\times$ 118 (Ref. 53 $\times$ 117.7).
 Fig. 5. *Cyclogranisporites lasius* (Waltz) Playford 1962. Slide O3V16–3 (6), location 28 $\times$ 111.6 (Ref. 33 $\times$ 117.9).
 Figs. 6, 7. *Granulatisporites* cf. *pallidus* Kosanke 1950. 6, Proximal surface; Slide O3V16–3 (5), location 13.9 $\times$ 115.1 (Ref. 33.7 $\times$ 118). 7, Proximal surface; Slide O3V16–3 (6), location 23.5 $\times$ 123 (Ref. 33 $\times$ 117.9).
 Figs. 8, 9. *Granulatisporites politus* Hoffmeister, Staplin, and Malloy 1955. 8, Proximal surface; Slide O3V16–3 (5), location 43.7 $\times$ 108 (Ref. 33.7 $\times$ 118). 9, Proximal surface; Slide O3V16–11 (R-1), location 29 $\times$ 93 (Ref. 31.7 $\times$ 116.9).
 Fig. 10. *Granulatisporites spinosus* Kosanke 1950. Distal surface; Slide O3V16–3 (5), location 24.9 $\times$ 128.4 (Ref. 33.7 $\times$ 118).
 Fig. 11. *Anapiculatisporites concinnus* Playford 1962. Distal surface; Slide O3V16–14 (6), location 10.2 $\times$ 108.6 (Ref. 33 $\times$ 117).
 Figs. 12, 13. *Lophotriteles labiatus* Sullivan 1964. 12, Proximal surface; Slide O3V17–1 (4), location 44 $\times$ 117.2 (Ref. 32 $\times$ 119.6). 13, Proximal surface; Slide O3V16–3 (A-2), location 25.9 $\times$ 125 (Ref. 32.2 $\times$ 117.9).
 Figs. 14, 15. *Granulatisporites tuberculatus* Hoffmeister, Staplin, and Malloy 1955. 14, Distal surface; Slide O3V16–13 (B-1), location 49.2 $\times$ 119.4 (Ref. 31.9 $\times$ 117.2). 15, Proximal surface; Slide O3V16–4 (R-1), location 27.5 $\times$ 96.6 (Ref. 32.3 $\times$ 118.7).



FELIX and BURBRIDGE, Carboniferous miospores (Springer fm)

Calamospora cf. *parva* Guennel 1958

Plate 53, fig. 17

Description. Trilete, spherical, with numerous lenticular folds. Laesurae short, 7.5–13 μ in length (average 8–10 μ), no visible lips. Wall laevigate, not exceeding 1 μ in thickness. Well-developed *area contagionis*.

Dimensions. (50 specimens.) Equatorial diameter 25–45 μ (average 35–40 μ).

Discussion. This spore is quite common throughout the Springer section, and its probable assignment to *C. parva* is based on a close comparison but without certainty that they are conspecific. The Springer form could probably be fitted into other specific niches available in the published literature. The presence of the *area contagionis* is of doubtful value, being noted in several other species. A significant clue as to the possible true nature of many small *Calamospora* may again be provided by the results of Hartung (1933) and his description of the numerous degenerate spores from *Macrostachya* cones. There is little doubt in the present authors' opinion but that *C. cf. parva* represents such degeneracy or immature developmental stage.

Genus WALTZISPORA Staplin 1960

Type species. *W. lobophora* (Waltz) Staplin 1960.

Waltzispora sagittata Playford 1962

Plate 53, fig. 18

1960 *Leiotriletes politus* Love, p. 111, pl. 1, fig. 1.

1962 *Waltzispora sagittata* Playford, p. 582, pl. 79, fig. 12, text-fig. 5c.

Description. Radial, trilete, subtriangular with concave interradial margins and convex apices. Laesurae simple, length three-fourths of spore radius, occasionally extending to body margin. Wall about 1 μ thick, laevigate to finely granulose.

Dimensions. (15 specimens.) Equatorial diameter 24–30 μ .

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Genus GULISPORITES Imgrund 1960

Type species. *G. cochlearius* (Imgrund) Imgrund 1960.

Gulisporites incomptus sp. nov.

Plate 54, fig. 3

Diagnosis. Radial, trilete, subtriangular, with slightly convex sides and rounded apices. Laesurae prominent, extending nearly to body margin, lips dark, commissures usually obscured by lips; lips 13–15 μ wide, 5–8 μ high, frequently contorted to appear spirally twisted. Body laevigate, wall indistinct and relatively thin, not exceeding 2.5 μ .

Dimensions. (25 specimens.) Equatorial diameter 50–80 μ (average 60–70 μ).

Holotype. Slide O3V16–9 (A–1). Location 27.9 $\times$ 119 (Ref. 31 $\times$ 116.5).

Description. Holotype $60 \times 65 \mu$, subtriangular with slightly convex sides. Prominent laesurae, non-dehiscent; lips 6μ high and 16μ wide. Exine laevigate, width indistinct.

Discussion. This species differs relatively little from *G. torpidus* described by Playford (1964) from the Mississippian Horton group. *G. torpidus* was granulose in some instances and possessed conspicuous lips which broadened noticeably towards the equator, while the lips of *G. incomptus* are relatively uniform throughout. *G. torpidus* is also noted as having a thick exine, whereas *G. incomptus* has a rather thin wall which is usually difficult to discern. This spore is almost certainly the same which Love (1960) designated as *Ahrensia sporites* type B from the Lower Carboniferous of Scotland. However, the prominent laesurae are not regarded as being comparable to kyrtomes.

Genus *HADROHERCOS* gen. nov.

Type species. *H. stereon* sp. nov.

Diagnosis. Radial, trilete, subtriangular with very rounded corners. Laesurae straight with prominent, unornamented lips. The spore wall consists of two layers. The inner layer is formed of closely packed, occasionally fused, verrucae with irregular bases; and the outer layer which is a sheath-like covering resting directly on top of the verrucae. This outer layer of the wall contains canals causing it to be very subject to corrosion. Often large patches of it are gone, revealing the negative reticulum formed by the verrucae beneath. Prominent lips and the unusual wall structure characterize the genus.

Hadrohercos stereon sp. nov.

Plate 65, figs. 1-3

Diagnosis. Radial, trilete, subtriangular with very rounded corners. Laesurae straight, $50-63 \mu$ long, with smooth lips $11-13 \mu$ wide. Pitting usually develops along the edge of the lips. The verrucae composing the inner wall layer are $2-6 \mu$ high and have irregularly shaped bases ranging from somewhat polygonal ($2-3 \mu$ across) to slightly elongated ($1 \times 4 \mu$). They are closely packed ($1-2 \mu$ between) and occasionally fused. The outer wall layer is $5-6 \mu$ thick and contains canals 1μ or less in diameter. These canals can be seen easily in side view (Pl. 65, fig. 3) and plan view (Pl. 65, fig. 2). The outer sheathing is often partially corroded revealing the negative reticulum formed by the verrucae beneath.

Dimensions. (7 specimens.) Equatorial diameter $126-50 \mu$ (average 140μ).

Holotype. Slide O3V16-10 (2). Location 23.5×114 (Ref. 53 $\times$ 117.7).

Description. Holotype $144 \times 144 \mu$ radial, trilete, subtriangular. Laesurae straight, $50-55 \mu$ long. Lips 11μ wide with pitting on outer edge. Verrucae about 1μ apart and 6μ high with irregular bases. Large corroded patches reveal negative reticulum. Wall canals visible about 1μ wide. Outer layer of wall 5μ thick.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Infraturma APICULATI (Bennie and Kidston) Potonié and Kremp 1954

Genus CYCLOGRANISPORITES Potonié and Kremp 1954

Type species. *C. leopoldi* (Kremp) Potonié and Kremp 1954.

Cyclogranisporites lasius (Waltz) Playford 1962

Plate 54, fig. 5

1884 Type 524 of Reinsch, p. 52, pl. 32, fig. 211; pl. 42, fig. 220.

1938 *Azonotriletes lasius* Waltz in Lubert and Waltz, p. 9, pl. 1, fig. 4; pl. A, fig. 4.

1955 *Filicitriletes lasius* (Waltz) Lubert, p. 55, pl. 2, fig. 50.

1962 *Cyclogranisporites lasius* (Waltz) Playford, p. 585, pl. 79, figs. 19, 20.

Description. Radial, trilete. Laesurae simple, up to $24\ \mu$ in length, about two-thirds spore radius; often obscured by closely spaced, granulose sculpture elements and difficult to discern. Wall thin, $1\text{--}2.5\ \mu$ thick, with occasional folds; densely covered by fine granulose elements $1\text{--}1.5\ \mu$ in height. Sculpture elements variable, with some truncated and others tapered to varying degrees.

Dimensions. (25 specimens.) Equatorial diameter $55\text{--}75\ \mu$.

Discussion. It resembles *Cyclobaculisporites grandiverrucosus*, but the sculpture elements are very densely spaced and do not possess the uniformity of *Cyclobaculisporites*. The elements of the same specimen are often truncated as in *Cyclobaculisporites* or tapered in the manner of *Verrucosporites* as defined by Bhardwaj (1955).

Genus GRANULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *G. granulatus* Ibrahim 1933.

Granulatisporites cf. *pallidus* Kosanke 1950

Plate 54, figs. 6, 7

Description. Radial, trilete, triangular with rounded apices, interradial areas slightly concave. Laesurae distinct, straight, length two-thirds to three-fourths spore radius; no lip development, but a vague proximal contact area sometimes present. Proximal and distal ornamentation of closely spaced, minute granulations, about $1\ \mu$ in diameter and usually less than $1\ \mu$ in height. Spore wall (excluding granulations) about $1\ \mu$ thick.

Dimensions. (25 specimens.) Equatorial diameter $24\text{--}42\ \mu$.

Discussion. The Springer specimens have a gradation through specimens closely comparable to *G. commissuralis*, *G. granularis*, and *G. pallidus* Kosanke (1950). A clearcut separation is difficult to make, and the majority appear most closely referable to *G. pallidus*. Hoffmeister, Staplin, and Malloy (1955b, p. 389) encountered a similar situation. Kosanke separated the species on size and spacing of granulations but gave no precise measurements, using descriptive terms such as *coarsely granulose*, *distinctly granulose*, or *granulations are numerous and closely spaced which gives the spore a rough appearance*. His species were conveniently separated geologically but such is not the case in the Springer.

Granulatisporites politus Hoffmeister, Staplin, and Malloy 1955

Plate 54, figs. 8, 9

Description. Radial, trilete, subtriangular with bluntly rounded apices and concave sides. Laesurae distinct, straight, simple, extending nearly to body margin. Wall 1–2 μ thick, laevigate to minutely punctate.

Dimensions. (20 specimens.) Equatorial diameter 24–36 μ .

Discussion. The lateral projection of the rounded apices to produce an angular junction of the radial and interradial areas as described by Butterworth and Williams (1958) is largely the basis for assignment to this species. This is a constant feature of the Springer specimens.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Granulatisporites spinosus Kosanke 1950

Plate 54, fig. 10

1950 *Granulatisporites spinosus* Kosanke, p. 22, pl. 3, fig. 7.

1955 *Anapiculatisporites spinosus* (Kosanke) Potonié and Kremp, p. 82, pl. 14, figs. 253–5.

1957 *Spinotriletes sentus* Dybová and Jachowicz, pp. 130–1, pl. 32, fig. 3.

Dimensions. (20 specimens.) Equatorial diameter 30–38 μ . Spines acute, 2.5–5 μ long and 1.5 μ wide at bases.

Discussion. Kosanke's (1950) original designation is retained since it most adequately provides for the inclusion of this species, while the revision of Potonié and Kremp (1954) fails to sufficiently establish clear differences for genera such as *Apiculatisporis*, *Acanthotriletes*, *Anapiculatisporites* and *Lophotriletes*. The treatment by Dybová and Jachowicz (1957) is procedurally incorrect, and failure to retain the specific epithet violated the International Rules of Botanical Nomenclature.

Granulatisporites tuberculatus Hoffmeister, Staplin, and Malloy 1955

Plate 54, figs. 14, 15

Description. Radial, trilete, subtriangular with rounded apices and concave sides. Laesurae distinct, straight, simple, extending three-fourths of spore radius. Proximal and distal surfaces ornamented with blunt, conical tuberculae 0.5–2.5 μ in height, 1–3 μ wide at bases and 1–4 μ apart.

Dimensions. (25 specimens.) Equatorial diameter 30–45 μ .

Discussion. The Springer specimens project the size range of the species slightly, and tuberculae dimensions are added.

Genus *LOPHOTRILETES* (Naumova) Potonié and Kremp 1954

Type species. *L. gibbosus* (Ibrahim) Potonié and Kremp 1954.

Lophotriletes coniferus Hughes and Playford 1961

Plate 55, figs. 1, 4

Description. Radial, trilete, subtriangular to subcircular. Laesurae distinct, slightly sinuous, three-fourths of spore radius, extending to body margin occasionally. Coni up to $2\ \mu$ high and $1\text{--}4\ \mu$ apart. Body minutely granulose with one or two large folds.

Dimensions. (15 specimens.) Equatorial diameter $83\text{--}115\ \mu$.

Discussion. The only noteworthy difference from the description of Hughes and Playford is in the distribution of the coni. The Springer specimens appear to have slightly shorter coni and have them more closely spaced than in the type description.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Lophotriletes labiatus Sullivan 1964

Plate 54, figs. 12, 13

Description. Radial, triangular, with slightly convex sides, apices rounded. Laesurae straight, extending to body margin, prominent lips $4\text{--}6\ \mu$ wide on either side of laesurae. Proximal and distal surfaces ornamented with blunt cones about $1\ \mu$ in height.

Dimensions. (10 specimens.) Equatorial diameter $30\text{--}45\ \mu$.

Lophotriletes obtusus sp. nov.

Plate 55, figs. 5–7

Diagnosis. Radial, trilete, subtriangular, margins straight or slightly concave. Laesurae simple, extending three-fourths of radius, usually obscured by ornamentation. Ornamented proximally and distally by prominent projections of variable sizes and shapes; projections $1.5\text{--}7.5\ \mu$ in length, $1\text{--}6\ \mu$ in diameter across polygonal bases; apices rounded, bluntly squared, rarely acute; closely spaced, $1\text{--}3\ \mu$ apart. Projections tend to fuse, especially at spore apices, occasionally forming apical pads to $15\ \mu$ in length and $5\ \mu$ in width. Spore wall thin, $1\text{--}2\ \mu$.

Dimensions. (35 specimens.) Equatorial diameter (including projections) $35\text{--}50\ \mu$.

Holotype. Slide O3V16–11 (6). Location 54.5×125.2 (Ref. 31.7×116.9).

Description. Holotype radial, trilete, sides straight, apices rounded. Equatorial diameter $42 \times 42\ \mu$. Laesurae three-fourths of radius, obscured by ornamentation. Spore covered proximally and distally with blunt projections from $1.5\text{--}7.5\ \mu$ in length (average $3\ \mu$) and $2.5\ \mu$ in basal diameter. There is a slight fusion of projections at the apices, one forming a thickened apical pad $10\ \mu$ in length and $5\ \mu$ wide.

Discussion. The tendency of the projections to fuse is not consistent and varies from specimen to specimen. The greater fusion is at the apices and sometimes presents a superficial resemblance to *Triquitrites*. Some specimens show no fusion and seldom will it concern more than one apex of a specimen; very rarely all three apices will display some thickening. The holotype (Pl. 55, fig. 6) is markedly thickened at one apex.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus ANAPICULATISPORITES Potonié and Kremp 1954

Type species. *A. isselburgensis* Potonié and Kremp 1954.

Anapiculatisporites concinnus Playford 1962

Plate 54, fig. 11

Description. Radial, trilete, triangular with rounded apices and interrarial margins straight to convex. Laesurae distinct, simple, straight, length about four-fifths spore radius. Laevigate proximally; distal surface bearing small, scattered spines about $2\ \mu$ in length and $2\text{--}3\ \mu$ apart.

Dimensions. (10 specimens.) Equatorial diameter $20\text{--}43\ \mu$.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Genus RAISTRICKIA (Schopf, Wilson, and Bentall) Potonié and Kremp 1954

Type species. *R. grovensis* Schopf in Schopf, Wilson, and Bentall 1944.

Raistrickia vulgata sp. nov.

Plate 55, figs. 2, 3

Diagnosis. Radial, trilete. Laesurae straight, simple, $20\text{--}25\ \mu$ in length, extending two-thirds distance of body radius. Body densely covered with blunt spines, $2\text{--}5\ \mu$ in width

EXPLANATION OF PLATE 55

All figures $\times 500$ unless otherwise indicated.

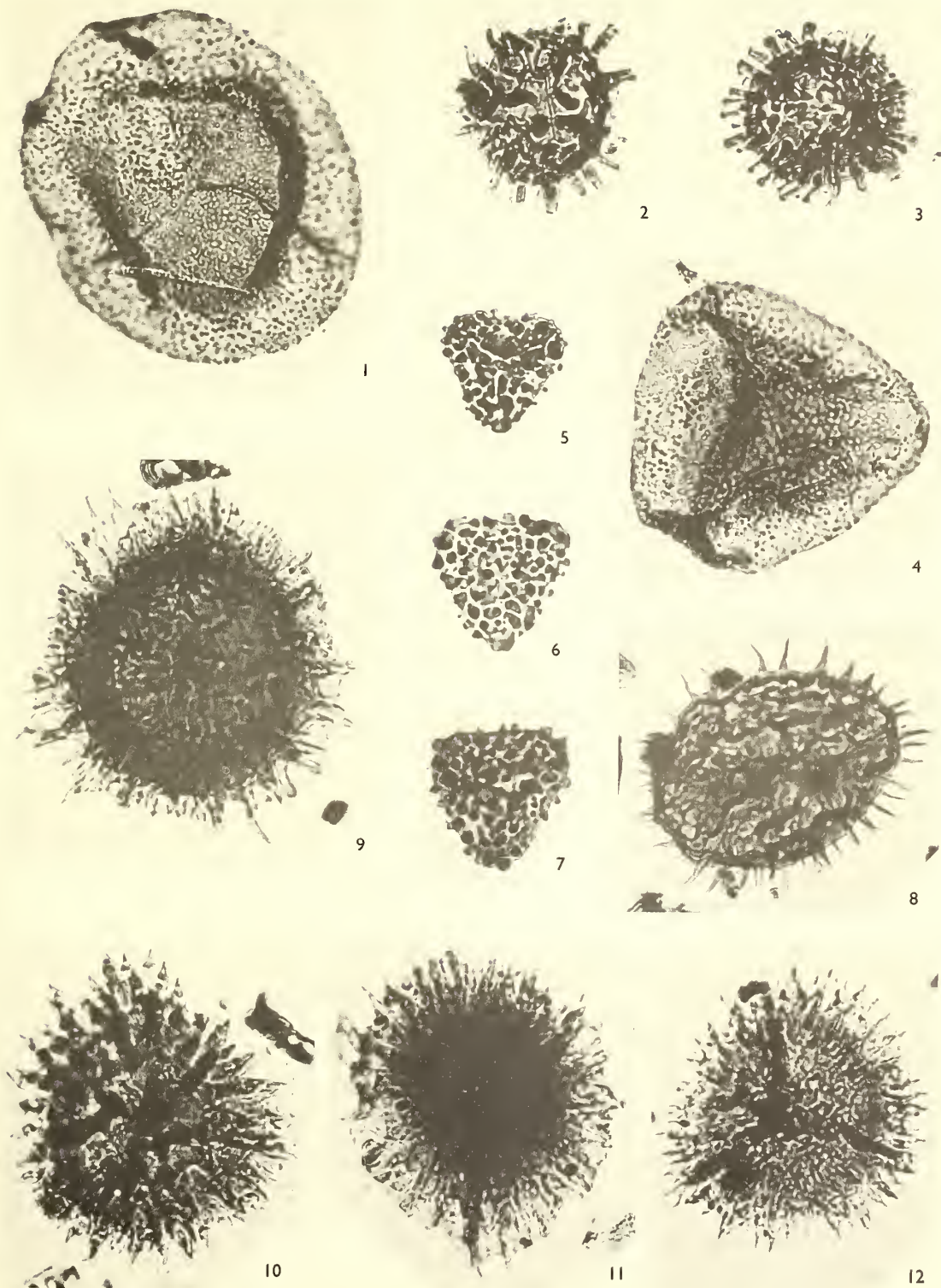
Figs. 1, 4. *Lophotrilletes coniferus* Hughes and Playford 1961. 1, Proximal surface; Slide O3V16-14 (6), location 46.8×122.5 (Ref. 33×117). 4, Distal surface; Slide O3V16-14 (6), location 17.4×125.9 (Ref. 33×117).

Figs. 2, 3. *Raistrickia vulgata* sp. nov. 2, Proximal surface; Slide O3V16-11 (6), location 38×119.8 (Ref. 31.7×116.9). 3, Holotype. Slide O3V16-11 (6), location 42×111.5 (Ref. 31.7×116.9).

Figs. 5-7. *Lophotrilletes obtusus* sp. nov. 5, Proximal surface; Slide O3V16-3 (5), location 15×116.8 (Ref. 33.7×118). 6, Holotype. Distal surface; Slide O3V16-11 (6), location 54.5×125.2 (Ref. 31.7×116.9). 7, Distal surface; Slide O3V16-5 (3), location 23.4×113.9 (Ref. 33.7×118.2).

Fig. 8. *Ibrahimisporites sentus* sp. nov. Holotype. Slide O3V16-3 (1), location 35×117.6 (Ref. 33×117.1).

Figs. 9-12. *Spinizonotriletes procinctus* sp. nov. 9, Holotype. Distal surface; Slide O3V16-11 (7), location 35×112.8 (Ref. 31.9×117.9). 10, Proximal surface; Slide O3V16-3 (5), location 29×122 (Ref. 33.7×118). 11, Distal surface; Slide O3V16-11 (7), location 27.8×128 (Ref. 31.9×117.9). 12, Proximal surface; Slide O3V16-11 (2), location 45.5×121.5 (Ref. 32×118).



FELIX and BURBRIDGE, Carboniferous miospores (Springer fm)

and 6–13 μ in length; individual spines are of uniform width and rarely show taper; apex of each spine minutely partite, best seen at high magnification. Spore coat thin, about 1 μ in thickness.

Dimensions. (25 specimens.) Equatorial diameter (including spines) 55–70 μ . Body diameter 40–53 μ .

Holotype. Slide O3V16–11 (6). Location 42 $\times$ 111.5 (Ref. 31.7 $\times$ 116.9).

Description. Holotype circular, over-all diameter 55 $\times$ 60 μ , body 44 $\times$ 46 μ . Laesurae two-thirds of radius. Spines uniformly distributed, 2.5–6.5 μ wide and 7.5–15 μ long, minutely partite.

Comparison. There is actually very little to distinguish a number of *Raistrickia* species other than spine characters, and this is an admittedly tenuous feature. *R. vulgata* compares well with *R. saetosa* (Loose) Schopf, Wilson, and Bentall as described by Potonié and Kremp (1955), but it does not have the differential proximal-distal spine distribution noted for *R. saetosa* by Bhardwaj (1957, pl. 23, fig. 20). *R. aculeata* Kosanke has similar dimensions but is described as having tapering or blunt spines. Likewise, *R. crinita* Kosanke has tapering, blunt spines and laesurae somewhat longer than in *R. vulgata*. *R. superba* (Ibrahim) Schopf, Wilson, and Bentall is comparable to the Springer species in size of body and spines but has rays reaching the body margin and truncate spines. There is every likelihood that a thorough, monographic study of the genus would result in conspecificity with some species presently described. However, its relatively stable and easily recognized characters, and its common occurrence in the Springer sediments, warrant recognition of *R. vulgata* at this time.

Genus IBRAHIMISPORES Artüz 1957

Type species. *I. microhorridus* Artüz 1957.

Ibrahimisporos sentus sp. nov.

Plate 55, fig. 8

Diagnosis. Radial, trilete, outline circular. Laesurae indistinct, simple, extending nearly to body margin. Ornamentation of hollow spines, up to 18 μ in length and 2–5 μ wide at base, tapering to acute tip; 30–40 spines occur about the equatorial outline; spines rarely recurved at the tips or with hollow, bulbous bases. Wall distinct, laevigate, 3–4 μ thick.

Dimensions. (10 specimens.) Over-all equatorial diameter 70–110 μ .

Holotype. Slide O3V16–3 (1). Location 35 $\times$ 117.6 (Ref. 33 $\times$ 117.1).

Description. Holotype 73 $\times$ 100 μ over-all, irregularly circular. Laesurae obscured by folds of exine, simple, extending nearly to margin. Spines hollow, up to 12 μ in length, 2–4 μ wide at base, tapering to acute tip. About 35 spines occurring about equatorial outline. Wall distinct, laevigate, 3 μ thick.

Comparison. *I. sentus* resembles *I. microhorridus* Artüz 1957. However, the latter appears to have solid spines, and the spines are considerably broader with relationship to length.

Artüz (*personal communication*) in an examination of the Springer material did not consider the specimens referable to her *I. microhorridus*. The only other described species showing any comparison to *I. sentus* is *I. brevispinosus* Neves 1961, but it differs in its stout, hollow spines with solid tips.

Genus SPINOZONOTRILETES Hacquebard 1957

Type species. S. uncatus Hacquebard 1957.

Spinozonotriletes procinctus sp. nov.

Plate 55, figs. 9–12

Diagnosis. Radial, trilete, roundly subtriangular. Laesurae obscure to distinct, slightly sinuous, lips to $3.5\ \mu$ wide on either side of commissure, rays extending to body margin. Spore differentiated into sculptured outer membrane and an enclosed central 'body'. Outer membrane variable from slight to very thick and extending beyond the body to form a wide flange-like structure. Spinose sculpture restricted to the distal surface and equatorial area, proximal surface very rarely displays vestigial spines. Spines variable in size and structure, $6\text{--}18\ \mu$ long and $2\text{--}4.5\ \mu$ wide at the base, densely spaced with 40–60 elements visible at the equatorial outline. Spines vary from acute, hollow to specimens with enlarged, bulbous bases with solid apices appearing as dark terminations. Spines are usually straight but recurved examples are sometimes present. The enlarged, swollen bases are usually associated with elements bearing dark, solid apices. Spines do bifurcate infrequently. Although the specific spine types generally seem to be associated with individual specimens, there are usually a few examples of all on each specimen. There is no clearcut basis for separation on spine morphology, and a gradual gradient exists from the rather simple, hollow, acute spines to the more complex, bulbous-based, solid-pointed spines. Spore size bears no significance to spine patterns as all spine types occur on spores of all dimensions. In an examination of *S. uncatus* Hacquebard, Playford (1963) considered the wide variation in spine dimensions as being between specimens rather than within specimens. Despite the variety of spines noted in the Springer specimens and the appearance of more than one form on a specimen, Playford's findings apply to them. Individual specimens do bear spines of fairly uniform size and structure, and morphological variations on individual specimens are minor and usually obscure.

Dimensions. (100 specimens.) Over-all equatorial diameter $85\text{--}140\ \mu$. When distinct, central body diameter $65\text{--}75\ \mu$.

Holotype. Slide O3V16–11 (7). Location 35×112.8 (Ref. 31.9×117.9).

Description. Holotype $110 \times 110\ \mu$ over-all, roundly subtriangular. Prominent, laevigate, membranous perispore presenting appearance of flange; body distinct and $72 \times 73\ \mu$ in diameter. Sinuous rays extending to body margin. Prominent spines distributed equatorially and distally, acute, hollow, up to $10\ \mu$ in length and to $4.5\ \mu$ wide basally; about 40 spines occurring equatorially.

Discussion. Playford (1963) has discussed the problem of terminology and morphology of the genus to a considerable extent, and he questions whether a true perispore (perine) is present. He recognized an exoexine and intexine in his discussion of *Spinozonotriletes*.

In a later work, Dettmann and Playford (1963) demonstrated that the exoexine in *S. uncatus* Hacquebard has the spinose sculpture and forms the elevated lips of the laesurae.

Comparison. The only previously described species of the genus that is anyway similar to *S. procinctus* is *S. uncatus* Hacquebard 1957. However, *S. uncatus* has a smaller number of body spines and a difference in spine distribution. *S. procinctus* is rather densely ornamented with spines, with 40–60 usually being observed about the equator, whereas Hacquebard (1957) reports about 21 spines occurring equatorially. He also recorded their occurrence both proximally and distally, while in *S. procinctus* they are restricted to the distal side and equatorial area. *S. procinctus* also seems to have a much greater development of the perispore than any other species.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Genus MOOREISPORITES Neves 1958

Type species. *M. fustus* Neves 1958.

Mooreisporites lucidus (Artüz) comb. nov.

Plate 56, fig. 1

1957 *Tripartites lucidus* Artüz p. 249, pl. 4, fig. 29.

1959 *Tripartites lucidus* Artüz p. 43, pl. 7, fig. 42.

Description. Radial, trilete, concavely subtriangular. Laesurae straight, over one-half of radius, slight lip development; sutures frequently split to form triangular opening with rolled edges giving false impression of thickened lips. Thickened apical pads $10 \times 20 \mu$ to $15 \times 30 \mu$, bearing numerous projections, which are often fused basally and branch apically, individual projections $1.5\text{--}2.5 \mu$ wide and up to 7μ in length. Exine thin, not exceeding 1μ ; surface laevigate.

Discussion. The spore described by Artüz (1957, 1959) from the Westphalian A as *Tripartites lucidus* agrees with the Springer representative in every respect, and Sullivan and Neves (1964) have rejected *Tripartites lucidus* from *Tripartites*.

Comparison. *M. lucidus* differs from previously described species on exine ornamentation features alone. *M. trigallerus* Neves 1961 has numerous scattered coni. *M. bellus* Neves 1961 also possesses scattered coni, as well as large baculae which develop extensively over the distal surface, while *M. fustus* Neves 1958 bears distal, branching baculae.

Mooreisporites trigallerus Neves 1961

Plate 56, fig. 2

Description. The thickened pads at the apices formed by fusion of the baculae range from $19\text{--}35 \mu$ in width; they are $7\text{--}15 \mu$ high including pad and projections. The individual baculae are $6\text{--}9 \mu$ in length.

Dimensions. (10 specimens.) Over-all equatorial diameter $60\text{--}75 \mu$.

Genus CYCLOBACULISPORITES Bhardwaj 1955

Type species. *C. grandiverrucosus* (Kosanke) Bhardwaj 1955.

Cyclobaculisporites grandiverrucosus (Kosanke) Bhardwaj 1955

Plate 56, fig. 3

1943 *Punctatisporites grandiverrucosus* Kosanke, p. 127, pl. 3, fig. 4.

1955 *Cyclobaculisporites grandiverrucosus* (Kosanke) Bhardwaj, p. 123, pl. 1, fig. 1.

Description. Radial, trilete. Laesurae $18-21\ \mu$ in length, not exceeding two-thirds of radius; lips narrow, laesurae sometimes obscured by baculae. Margin of densely spaced baculae $1.5-2\ \mu$ high and $0.5-2\ \mu$ wide, 75–80 baculae visible about marginal periphery. Baculae of individual specimens of uniform height and of variable shapes in surface view.

Dimensions. (25 specimens.) Equatorial diameter $65-78\ \mu$.

Discussion. A slight adjustment in size range should be noted as Bhardwaj (1955) listed $70\ \mu$ as the lowermost limit. In view of the remarkable uniformity of the baculae on Springer specimens, the baculae character to differentiate the genus seems to warrant the significance given to it by Bhardwaj. The minute baculae have uniform truncated apices, and in surface section have the unequal sizes and irregular shapes illustrated in the genotype. It affords a means of removing the spore from the meaningless heterogeneity of *Punctatisporites*.

Genus GRANDISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *G. spinosa* Hoffmeister, Staplin, and Malloy 1955

Grandispora echinata Hacquebard 1957

Plate 56, figs. 4, 5

EXPLANATION OF PLATE 56

All figures $\times 500$ unless otherwise indicated.

Fig. 1. *Mooreisporites lucidus* (Artüz) comb. nov. Proximal surface; Slide O3V16-13 (A-2), location 43.8×112.8 (Ref. 32.2×117.9).

Fig. 2. *Mooreisporites trigallerus* Neves 1961. Proximal surface; Slide O3V16-13 (A-1), location 14.5×128 (Ref. 31.1×117.9).

Fig. 3. *Cyclobaculisporites grandiverrucosus* (Kosanke) Bhardwaj 1955. Proximal surface; Slide O3V16-11 (7), location 17.5×100 (Ref. 31.9×117.9).

Figs. 4, 5. *Grandispora echinata* Hacquebard 1957. 4, Tetrad; Slide O3V16-11 (7), location 23.2×125.3 (Ref. 31.9×117.9). 5, Distal surface; Slide O3V16-9 (5), location 51.7×126.9 (Ref. 32.4×118.6).

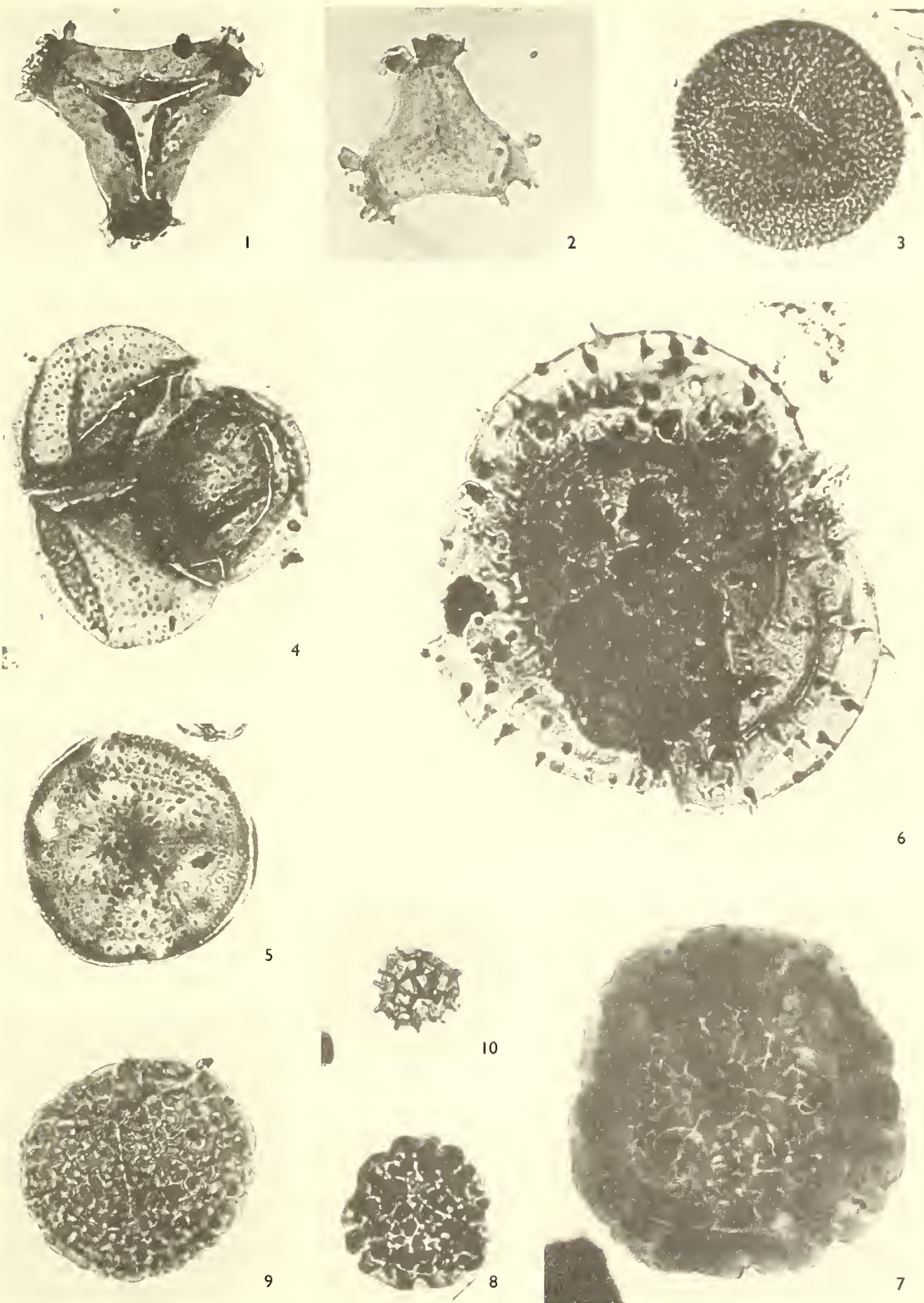
Fig. 6. *Grandispora spinosa* Hoffmeister, Staplin, and Malloy 1955. Tetrad; Slide O3V16-10 (B-1), location 42×112.5 (Ref. 32.5×117.9).

Fig. 7. *Convolutispora crassa* Playford 1962. Proximal surface; Slide O3V16-10 (A-1), location 46×122 (Ref. 29.5×118.2).

Fig. 8. *Convolutispora florida* Hoffmeister, Staplin, and Malloy 1955. Proximal surface; Slide O3V17-1 (4), location 43.8×103 (Ref. 32×119.6).

Fig. 9. *Convolutispora mellita* Hoffmeister, Staplin, and Malloy 1955. Proximal surface; Slide O3V16-4 (1), location 7.2×110.5 (Ref. 30.3×117.7).

Fig. 10. *Dictyotrilletes clatriformis* (Artüz) Sullivan 1964. Slide O3V16-3 (5), location 56.2×127.8 (Ref. 33.7×118).



FELIX and BURBRIDGE, Carboniferous miospores (Springer fm)

Description. Radial, trilete; central body enclosed by bladder and not always well defined. Laesurae not always distinct, extending to body margin, up to $38\ \mu$ in length; commissure generally visible and lips $3\text{--}4\ \mu$ wide. Body usually laevigate, rarely minutely granulose. Distal surface of spore and bladder bears small cones and spinose projections of variable dimensions and spacing. The projections in some cases consist of blunt protuberances up to $1\ \mu$ in height, $1\ \mu$ in basal diameter, and situated $1\text{--}6\ \mu$ apart. The usual ornamentation consists of tapering spines $1\text{--}3\ \mu$ long, $1\text{--}1.5\ \mu$ in basal diameter, and situated $2\text{--}6\ \mu$ apart. There are infrequent instances of spines exceeding $3\ \mu$ in length and with a slight tendency to be falcate. Rare instances existed of specimens bearing scattered spines on the proximal surface. The spores were observed frequently in tetrads, with the entire tetrad diameter ranging from $95\text{--}135\ \mu$.

Dimensions. (25 specimens.) Over-all equatorial diameter $60\text{--}80\ \mu$; diameter of spore body $54\text{--}60\ \mu$.

Discussion. This species is much smaller in over-all size than *G. spinosa*, the only other described species. The body and bladder are more clearly defined in *G. spinosa*, while the laesurae are more distinct in *G. echinata*. The spinose projections of *G. spinosa* are also much larger and situated further apart. Hacquebard (1957) does not mention the distribution of the processes as being limited to the distal side, but neither is this character noted in the genotype description. In all other features it compares closely with *G. echinata*.

Other occurrences. Surface Caney formation, upper Mississippian, Johnston County, Oklahoma.

Grandispora spinosa Hoffmeister, Staplin, and Malloy 1955

Plate 56, fig. 6

Description. Radial, trilete; central body enclosed by bladder, usually well defined; bladder and body wall thin and faintly granulose. Laesurae indistinct, appear to extend to body margin. Spore body and bladder surface bear spinose projections $3\text{--}7\ \mu$ long, $1\text{--}3\ \mu$ wide at base, and $6\text{--}16\ \mu$ apart; spines usually acute but occasionally blunt, usually straight but sometimes curved. Spines are present on both proximal and distal surfaces of body and bladder but are more densely developed on distal surface. Observed more frequently in tetrads, with entire tetrad being $130\text{--}60\ \mu$ in diameter.

Dimensions. (10 specimens.) Over-all equatorial diameter $90\text{--}125\ \mu$; diameter of spore body $70\text{--}95\ \mu$.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; subsurface Springer formation, Anadarko Basin; subsurface Chester formation, upper Mississippian, Anadarko Basin; surface Prairie Mountain and Wildhorse Mountain formations, Jackfork group, upper Mississippian, LeFlore County, Oklahoma.

Infraturma MURORNATI Potonié and Kremp 1954

Genus CONVOLUTISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *C. florida* Hoffmeister, Staplin, and Malloy 1955.

Convolutispora crassa Playford 1962

Plate 56, fig. 7

Description. Radial, trilete, circular. Wall thick, $9\text{--}16\ \mu$, including muri. Sculpture of

sinuous, flat muri, anastomosing to form imperfect reticulum; muri $3-8\ \mu$ long, $1-3\ \mu$ high. Laesurae simple, straight, length two-thirds of spore radius.

Dimensions. (15 specimens.) Equatorial diameter $60-110\ \mu$.

Convolutispora florida Hoffmeister, Staplin, and Malloy 1955

Plate 56, fig. 8

Description. Radial, trilete, circular to subcircular. Ornamentation of irregularly arranged, coarsely vermiculate ridges of variable shape; ridges $1-3\ \mu$ in height and $3-7\ \mu$ in width. Laesurae simple, straight, one-half to three-fourths spore radius, sometimes obscured by ornamentation.

Dimensions. (25 specimens.) Equatorial diameter $38-50\ \mu$.

Discussion. It is admittedly difficult at times to distinguish *C. florida* from species of *Secarisporites*, especially *S. remotus* which has a comparable size range. The pronounced lobation in *Secarisporites* and the presence of a body are the best differentiation features. However, when the body outline is indistinct, identification is difficult. Further study could certainly result in the establishment of a closer relationship between the two.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Convolutispora lepida sp. nov.

Plate 57, fig. 4

Diagnosis. Radial, trilete, circular to subcircular. Laesurae simple, straight, three-fourths of spore radius, usually obscured by sculpture. Wall thick, $7-12\ \mu$, including ridges; sculpture of closely packed, convoluted, freely anastomosing, flattened ridges. Ridges to $8\ \mu$ in height and $3-12\ \mu$ wide. Lumina irregular, up to $16\ \mu$ in length and $1-5\ \mu$ wide.

Dimensions. (20 specimens.) Equatorial diameter $50-75\ \mu$.

Holotype. Slide O3V16-11 (6). Location 51×112.5 (Ref. 31.7×116.9).

Description. Holotype $60 \times 60\ \mu$, circular; laesurae approximately three-quarters radius, indistinct due to ornamentation. Wall $12\ \mu$ thick; convolute ridges to $8\ \mu$ high and $4-9\ \mu$ wide, lumina narrow and to $16\ \mu$ in length.

Comparison. Some similarity is shown to *C. crassa* Playford 1962 (p. 594, pl. 81, figs. 10-12). However, *C. lepida* does not have the imperfect reticulum characteristic of *C. crassa*, is appreciably smaller, and laesurae features are less pronounced.

Convolutispora mellita Hoffmeister, Staplin, and Malloy 1955

Plate 56, fig. 9

Description. Radial, trilete, circular outline; laesurae simple, straight, $16-25\ \mu$ long, three-fourths spore radius, frequently obscured by ornamentation. Exine $3-7\ \mu$ thick,

uniformly sculptured with broad anastomosing ridges, usually flat surfaced, 2–3 μ high and 2–6 μ wide; interval between convolute ridges about 1 μ .

Dimensions. (50 specimens.) Equatorial diameter 54–80 μ .

Discussion. The only significant departure from the type description is in laesurae length. Hoffmeister, Staplin, and Malloy noted the rays as being 'slightly over one-half spore radius'. The laesurae of the Springer specimens were rather uniformly three-fourths the radius.

Convolutispora sculptilis sp. nov.

Plate 57, fig. 1

Diagnosis. Radial, trilete, circular; laesurae distinct, simple, straight, one-half to two-thirds spore radius, frequently obscured by sculpture. Wall 3–4 μ thick, uniformly sculptured with low, closely spaced, anastomosing ridges; muri not overlapping, 3–6 μ high, 2–9 μ wide. Lumina distinct, irregular in shape, ranging from rounded to elongate 4 $\times$ 4 μ to 3 $\times$ 12 μ . Equatorial margin undulate.

Dimensions. (10 specimens.) Equatorial diameter 55–75 μ .

Holotype. Slide O3V16–3 (6). Location 52.3 $\times$ 108.4 (Ref. 33 $\times$ 117.9).

Description. Holotype circular, 61 $\times$ 70 μ ; laesurae two-thirds radius; body wall 3 μ thick; sculpture of anastomosing ridges, proximally and distally; muri 3–5 μ high and 3–9 μ wide. Distinct lumina rounded to elongate, 4 $\times$ 4 μ to 4 $\times$ 10 μ .

Convolutispora superficialis sp. nov.

Plate 57, figs. 2, 3

Diagnosis. Radial, trilete, circular to subcircular, slight marginal undulation. Wall with indistinctly defined sculpture, forming weak convolutions; the elevated portions are broad, weakly developed, with little sinuosity or ramification evident. Weakly delimited lumina usually elongate, 1–5 μ wide and 8–15 μ long; lumina very shallow, not exceeding 2 μ and usually about 1 μ in depth. Laesurae generally distinct, straight, slight lip development, length two-thirds to three-fourths spore radius. Body wall 2–6 μ , well defined.

Dimensions. (50 specimens.) Equatorial diameter 54–80 μ .

Holotype. Slide O3V16–11 (5). Location 40 $\times$ 128 (Ref. 32.6 $\times$ 117.8).

Description. Holotype circular, 78 $\times$ 80 μ . Sculpture of slightly elevated, poorly defined, convolutions. Lumina about 1 μ in depth, ranging from 2.5 $\times$ 15 μ to 5 $\times$ 8 μ in dimensions. Laesurae 25–27 μ in length, over two-thirds radius, slight lip development, commissure distinct. Wall distinct, 6 μ thick.

Discussion. There has been some hesitancy in assignment of this spore to *Convolutispora*. The ornamentation cannot be regarded as ridge-like processes as described by Hoffmeister, Staplin, and Malloy (1955b). It is more in the nature of a shallow, irregular, scalloped effect. Nevertheless, the ornamentation pattern is a convolute one. The

elevated portion of the wall often covers considerable area, being measured up to sections $17 \times 45 \mu$ in dimension. No real anastomosing or branching occurs.

Convolutispora venusta Hoffmeister, Staplin, and Malloy 1955

Plate 57, fig. 7

Description. Radial, trilete, spherical; laesurae simple, straight, length two-thirds spore radius, occasionally four-fifths; sometimes obscured by sculpture. Wall thick, sculptured with irregular, arete ridges, some anastomosing to form irregular lumina; ridges $1-3 \mu$ high, $2-3 \mu$ wide at their bases.

Dimensions. (15 specimens.) Equatorial diameter $42-70 \mu$.

Convolutispora vermiformis Hughes and Playford 1961

Plate 57, fig. 5

Description. Radial, trilete. Coarsely rugulate sculpture of sinuous, ramifying muri; muri not intersecting and ridges rounded to flat. Lumina seldom delimited and irregular in size and shape when formed. Muri $2.5-12 \mu$ wide and up to 8μ in height. Laesurae

EXPLANATION OF PLATE 57

All figures $\times 500$ unless otherwise indicated.

Fig. 1. *Convolutispora sculptilis* sp. nov. Holotype. Proximal surface; Slide O3V16-3 (6), location 52.3×108.4 (Ref. 33×117.9).

Figs. 2, 3. *Convolutispora superficialis* sp. nov. 2, Holotype. Proximal surface; Slide O3V16-11 (5), location 40×128 (Ref. 32.6×117.8). 3, Proximal surface; Slide O3V16-9 (R-2), location 43×110.2 (Ref. 33.9×119.1).

Fig. 4. *Convolutispora lepida* sp. nov. Holotype. Proximal surface; Slide O3V16-11 (6), location 51×112.5 (Ref. 31.7×116.9).

Fig. 5. *Convolutispora vermiformis* Hughes and Playford 1961. Proximal surface; Slide O3V16-9 (A-1), location 44.7×111.3 (Ref. 31×116.5).

Fig. 6. *Reticulatisporites decoratus* Hoffmeister, Staplin, and Malloy 1955. Proximal surface; Slide O3V16-9 (A-1), location 17.5×111.5 (Ref. 31×116.5).

Fig. 7. *Convolutispora venusta* Hoffmeister, Staplin, and Malloy 1955. Proximal surface; Slide O3V16-3 (5), location 43.1×125 (Ref. 33.7×118).

Figs. 8, 9. *Reticulatisporites peltatus* Playford 1962. 8, Reticulum; Slide O3V16-9 (5), location 34×121 (Ref. 32.4×118.6). 9, Proximal surface; Slide O3V17-1 (3), location 35.5×121.9 (Ref. 31×119.5).

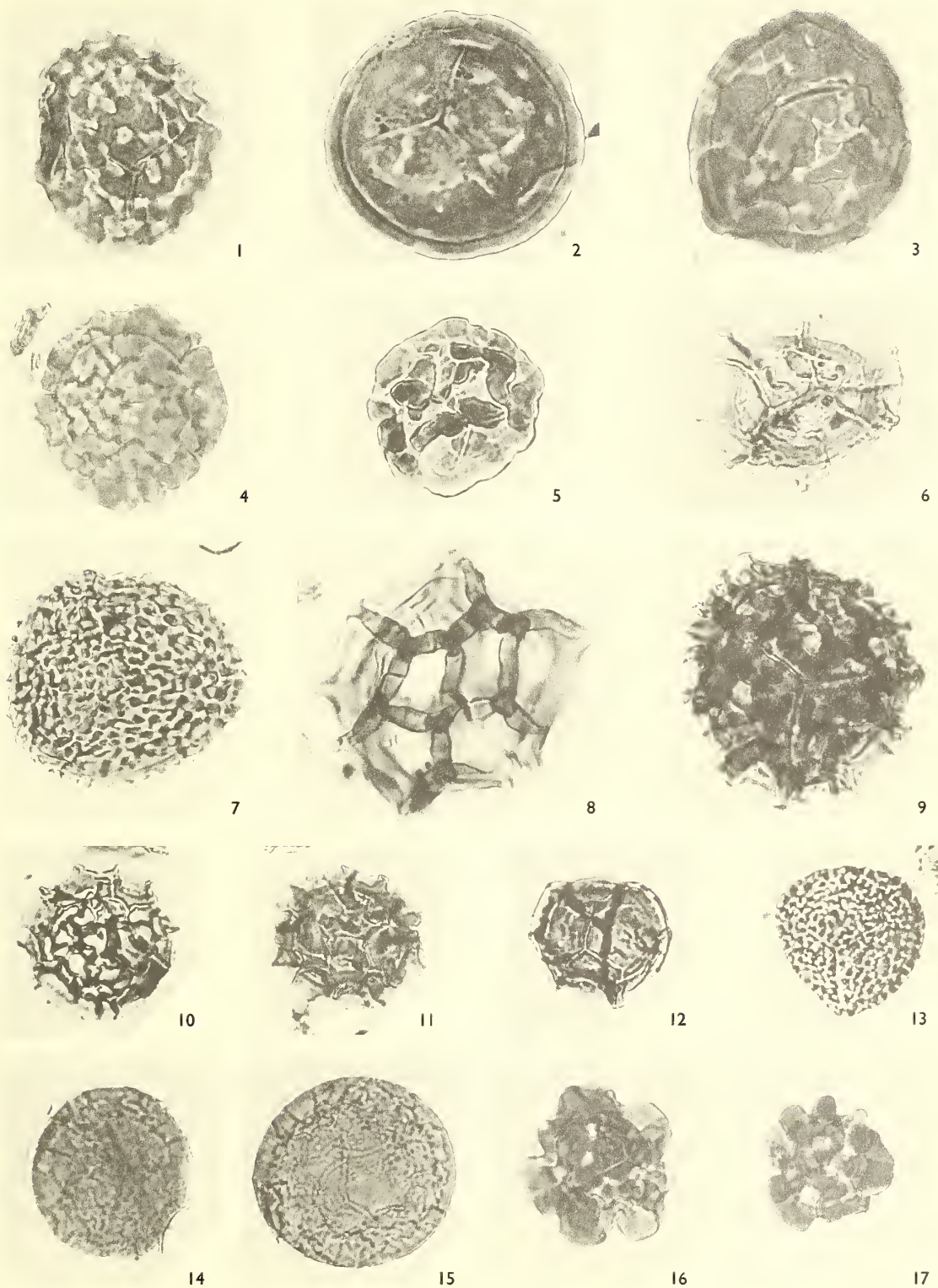
Figs. 10, 11. *Dictyotriteles pactilis* Sullivan and Marshall 1966. 10, Proximal surface; Slide O3V16-4 (R-1), location 52.6×107.8 (Ref. 32.2×117.2). 11, Proximal surface; Slide O3V16-3 (6), location 31.1×118.3 (Ref. 33×117.9).

Fig. 12. *Dictyotriteles insculptus* Sullivan and Marshall 1966. Distal surface; Slide O3V16-9 (5), location 26.5×123.8 (Ref. 32.4×118.6).

Fig. 13. *Foveosporites futilis* sp. nov. Holotype. Proximal surface; Slide O3V16-11 (6), location 40.2×124 (Ref. 31.7×116.9).

Figs. 14, 15. *Perotriteles perinatus* Hughes and Playford 1961. 14, Proximal surface; Slide O3V17-2 (1), location 51×117.2 (Ref. 31×117.9). 15, Distal surface; Slide O3V16-3 (2), location 45.4×114.7 (Ref. 29×118).

Figs. 16, 17. *Secarisporites remotus* Neves 1961. 16, Proximal surface; Slide O3V16-9 (B-2), location 11.4×126 (Ref. 31.7×118.2). 17, Distal surface; Slide O3V17-1 (3), location 10.8×125 (Ref. 31×119.5).



simple, straight, about two-thirds of radius and usually obscured by the sculpture. Body wall $2.5\text{--}5\ \mu$ thick, excluding muri. Lumina up to $20\ \mu$ in greatest dimension.

Dimensions. (15 specimens.) Equatorial diameter $40\text{--}70\ \mu$.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus *Dictyotriletes* (Naumova) Potonié and Kremp 1954

Type species. *D. bireticulatus* (Ibrahim) Potonié and Kremp 1954.

Dictyotriletes clatriformis (Artüz) Sullivan 1964

Plate 56, fig. 10

1957 *Reticulatisporites clatriformis* Artüz, p. 248, pl. 4, fig. 25a, b.

1959 *Reticulatisporites clatriformis* Artüz, p. 40, pl. 6, fig. 37a, b.

1964 *Dictyotriletes* cf. *clatriformis* (Artüz); Sullivan, p. 367, pl. 58, fig. 20; pl. 59, figs. 1, 2.

Description. Oval, trilete, rays difficult to discern. Muri about $1\ \mu$ wide and $1\text{--}2.5\ \mu$ high. Polygonal lumina $4\text{--}8.5\ \mu$ in maximum dimension.

Dimensions. (25 specimens.) Equatorial diameter $25\text{--}30\ \mu$.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Dictyotriletes pactilis Sullivan and Marshall 1966

Plate 57, figs. 10, 11

Description. Radial, trilete, oval. Muri $1\text{--}3\ \mu$ wide and $5\text{--}12\ \mu$ high. Lumina irregularly polygonal and $8\text{--}14\ \mu$ in diameter. Laesurae indistinct, usually obscured by reticulum, simple, and length two-thirds to three-fourths spore radius. Wall, excluding muri, $2\ \mu$ thick.

Dimensions. (20 specimens.) Equatorial diameter $44\text{--}66\ \mu$.

Discussion. Although Sullivan and Marshall (1966) did not observe trilete rays, they were definitely observed in the Springer specimens. However, measurable laesurae were very rare, and the ornamentation usually covered them.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnson County, Oklahoma.

Dictyotriletes insculptus Sullivan and Marshall 1966

Plate 57, fig. 12

Description. Radial, trilete, spherical. Laesurae indistinct, straight, slightly over one-half spore radius; simple, usually obscured by muri. Sculptured with delicately developed muri $1\text{--}2\ \mu$ wide enclosing polygonal to irregularly rounded lumina $6\text{--}20\ \mu$ in greatest diameter. Muri $2\text{--}3\ \mu$ high, translucent, and projecting in a manner to give the appearance of a narrow, membranous equatorial flange. Spore wall thin, $2\ \mu$ (exclusive of muri); laevigate except for rare and scattered granules.

Dimensions. (20 specimens.) Equatorial diameter $39\text{--}60\ \mu$.

Discussion. The loose reticulum is usually delimited into six to eight lacunae in each observed plane, and in undistorted specimens orientation results in a central polygonal lacuna with muri radiating outwards towards the spore periphery. There also appears to be a lesser number of lacunae proximally than on the distal side. *R. areolatus* Guennel 1958 is similar in general appearance but has a significantly different size range, as well as much smaller and more numerous lacunae.

Genus RETICULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *R. reticulatus* Ibrahim 1933.

Reticulatisporites decoratus Hoffmeister, Staplin, and Malloy 1955

Plate 57, fig. 6

Description. Radial, trilete, subcircular in outline. Laesurae indistinct, simple, length about two-thirds spore radius, usually obscured by muri. Muri high and membranous, presenting appearance of equatorial flange up to $12\ \mu$ in width; muri thin, $1\text{--}3.5\ \mu$. Lacunae irregular, $10\text{--}20\ \mu$ in longest diameter. Exine (excluding muri) $1.5\text{--}2.5\ \mu$ thick, occasionally with scattered granules.

Dimensions. (10 specimens.) Equatorial diameter $50\text{--}70\ \mu$.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Reticulatisporites peltatus Playford 1962

Plate 57, figs. 8, 9

Description. Laesurae distinct, extending almost to body margin, lips thin. Reticulum formed of rounded muri $3\text{--}8\ \mu$ wide and $3\text{--}4\ \mu$ high; polygonal lumina irregular and up to $17\ \mu$ in longest dimension. Peltate processes originate at junctions of muri; processes are $5\text{--}13\ \mu$ long and up to $10\ \mu$ wide at expanded apices. Body wall $2\ \mu$ thick. Reticulum more regular and lumina smaller on distal side, frequently loosely arranged proximally.

Dimensions. (25 specimens.) Equatorial diameter including processes $63\text{--}68\ \mu$, excluding processes $45\text{--}65\ \mu$.

Discussion. It is quite likely that *Raistrickia boleta* Staplin 1960 and *R. peltatus* are identical. However, the reticulate nature of the spore makes *Reticulatisporites* the more suitable repository, and the excellence of Playford's illustrations and descriptions permits a closer comparison with *R. peltatus*. Neither Staplin nor Playford mention the shape of the peltate processes when the expanded tips were viewed in a plane perpendicular to the body. In the Springer specimens the apices are triangular (Pl. 57, fig. 8), and a similar configuration is evident in Playford's illustrated specimens.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; subsurface Mississippian Chainman formation, Standard Continental Hayden Creek Unit No. 1 well, White Pine County, Nevada.

Genus FOVEOSPORITES Balme 1957

Type species. *F. canalis* Balme 1957.

Foveosporites futilis sp. nov.

Plate 57, fig. 13

Diagnosis. Radial, trilete, roundly triangular. Laesurae distinct, straight, length two-thirds to four-fifths spore radius. Commissure faint, but distinct at proper focus, no lip development. Spore coat densely ornamented with small pits $1\text{--}1.5\ \mu$ in diameter and spaced $1\text{--}3\ \mu$ apart. Spore wall distinct, $3\ \mu$ thick.

Dimensions. (10 specimens.) Equatorial diameter $42\text{--}50\ \mu$.

Holotype. Slide O3V16-11 (6). Location 40.2×124 (Ref. 31.7×116.9).

Description. Holotype $45 \times 46.5\ \mu$, roundly triangular; laesurae $15\text{--}21\ \mu$ long, three-fourths to four-fifths radius; wall $3\ \mu$ thick, covered with closely spaced circular pits $1\text{--}1.5\ \mu$ in diameter.

Discussion. This genus was established by Balme (1957) for circular or roundly triangular trilete spores with sculpture of pits or short channels irregularly distributed.

Comparison. *F. futilis* bears a decided resemblance to *Converrucosisporites sulcatus* (Wilson and Kosanke) Potonié and Kremp 1955. However, the Springer spore is definitely ornamented with circular, regularly spaced pits. Examination of numerous specimens of *C. sulcatus* from various localities and Pennsylvanian horizons revealed it to be quite verrucose-reticulate. Some conjecture exists over this spore as Guennel (1958, p. 61) has noted, but it is not pitted in the manner of *F. futilis*.

Genus SECARISPORITES Neves 1961

Type species. *S. lobatus* Neves 1961.

Secarisporites remotus Neves 1961

Plate 57, figs. 16, 17

Description. Radial, trilete, circular to subcircular. Ornamentation of irregular ridges. Peripheral lobes of varying dimensions extend to $10\ \mu$ beyond body wall and are up to $20\ \mu$ in width, lobes sometimes overlapping and deeply incised. Body distinct, $20\text{--}30\ \mu$ in diameter. Laesurae thin, straight, largely obscured by ornamentation.

Dimensions. (25 specimens.) Equatorial diameter $35\text{--}60\ \mu$.

Discussion. The authors are in agreement with Neves' (1961, p. 260) distinction of the genus from *Convolutispora*. The body outline is usually easily discerned in the Springer

specimens, and the peripheral rim formed by the lobes is quite distinct from the convolute ornamentation of *Convolutispora*.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus RETICULATASPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *R. facetus* Ibrahim 1933.

Reticulatasporites lacunosus sp. nov.

Plate 58, figs. 1, 2

Diagnosis. Spores radial, laesurae not visible. Sculptured with strongly developed muri $1.5\text{--}4.5\ \mu$ in width, enclosing polygonal to irregularly shaped lumina ranging from $3.5 \times 3.5\ \mu$ to $10 \times 15\ \mu$. Muri $3.5\text{--}7\ \mu$ high, occasionally muri terminated by slightly peltate enlargement. Spore wall $12\text{--}15\ \mu$ thick including height of muri.

Dimensions. (15 specimens.) Equatorial diameter $115\text{--}65\ \mu$.

Holotype. Slide O3V16-11 (7). Location 48.6×116.2 (Ref. 31.9×117.9).

Description. Holotype spherical, $144 \times 156\ \mu$ in diameter; laesurae not evident; deeply

EXPLANATION OF PLATE 58

All figures $\times 500$ unless otherwise indicated.

Figs. 1, 2. *Reticulatasporites lacunosus* sp. nov. 1, Holotype. Slide O3V16-11 (7), location 48.6×116.2 (Ref. 31.9×117.9). 2, Slide O3V16-10 (2), location 36.5×119 (Ref. 53×117.7).

Figs. 3, 4. *Tripartites dubitalis* sp. nov. 3, Holotype. Proximal surface; Slide O3V17-1 (5), location 44.8×127.8 (Ref. 32×119). 4, Proximal surface; Slide O3V17-1 (4), location 16.5×121.2 (Ref. 32×119.6).

Fig. 5. *Tripartites vetustus* Schemel 1950. Proximal surface; Slide O3V16-13 (A-1), location 44.6×114.2 (Ref. 31.1×117.9).

Fig. 6. *Ahrensisporites irroratus* sp. nov. Holotype. Proximal surface; Slide O3V17-1 (3), location 34.5×112 (Ref. 31×119.5).

Fig. 7. *Scutulum pusillum* sp. nov. Holotype. Proximal surface; Slide O3V16-9 (A-1), location 27.5×112 (Ref. 31×116.5).

Fig. 8. *Lycospora brevijuga* Kosanke 1950. Proximal surface; Slide O3V16-3 (1), location 12.2×107.5 (Ref. 33×117.1).

Figs. 9, 10. *Lycospora nitida* (Horst) Potonié and Kremp 1955. 9, Proximal surface; Slide O3V17-1 (4), location 19×126.8 (Ref. 32×119.6). 10, Proximal surface; Slide O3V16-11 (6), location 49.8×120 (Ref. 31.7×116.9).

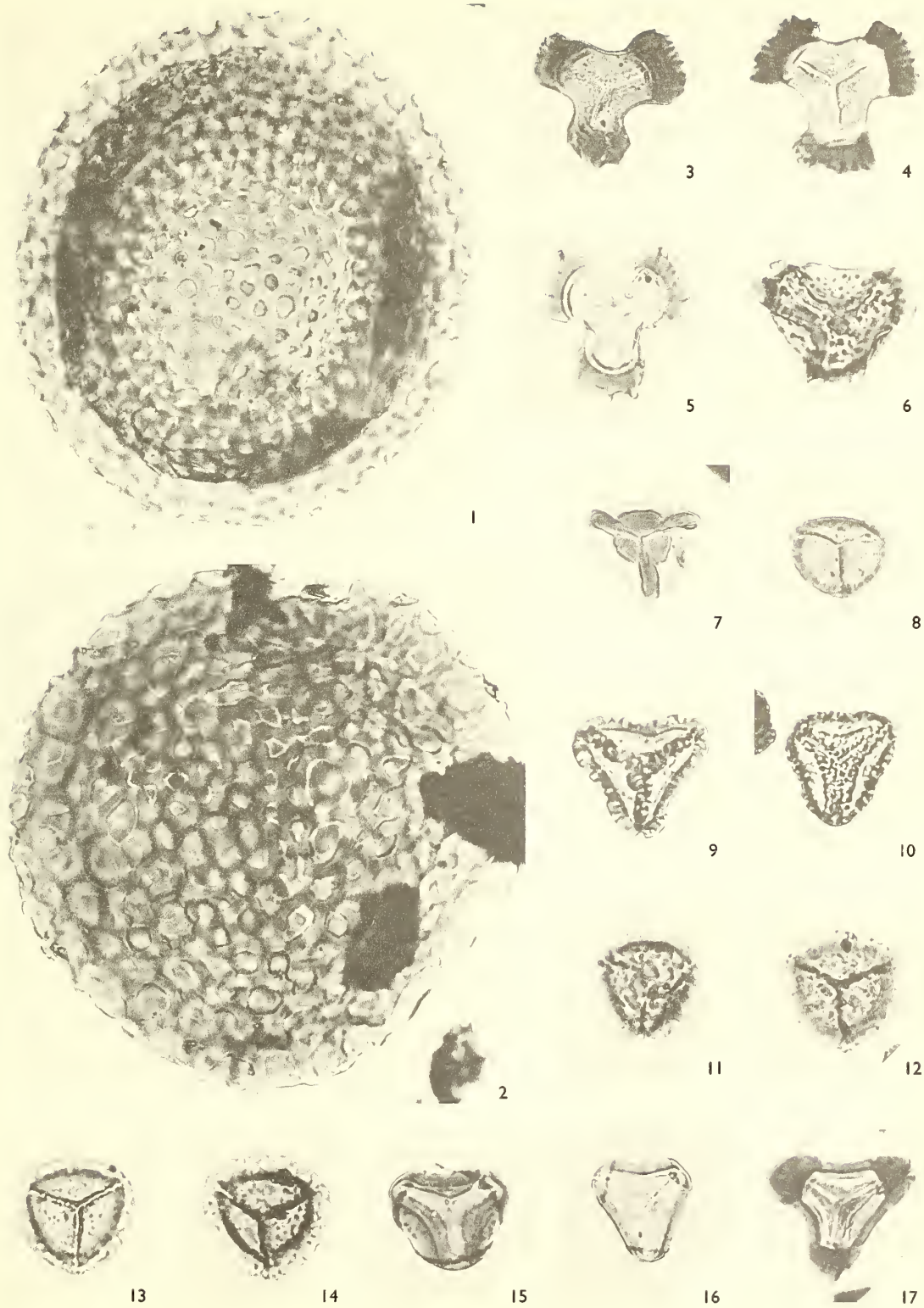
Figs. 11, 12. *Lycospora noctuina* Butterworth and Williams 1958. 11, Distal surface; Slide O3V16-13 (B-1), location 27.3×119.2 (Ref. 31.9×117.2). 12, Proximal surface; Slide O3V16-13 (B-1), location 48.9×121.5 (Ref. 31.9×117.2).

Fig. 13. *Lycospora pseudoannulata* Kosanke 1950. Proximal surface; Slide O3V16-3 (5), location 55×111.9 (Ref. 33.7×118).

Fig. 14. *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin 1960. Proximal surface; Slide O3V16-13 (B-1), location 42×123.1 (Ref. 31.9×117.2).

Figs. 15, 16. *Rotaspora fracta* Schemel 1950. 15, Proximal surface; Slide O3V16-9 (B-1), location 8.6×111 (Ref. 30.7×116.7). 16, Proximal surface; Slide O3V16-13 (5), location 23.6×116 (Ref. 31.3×118.3).

Fig. 17. *Simozonotrites intortus* var. *polymorphosus* Sullivan 1958. Proximal surface; Slide O3V16-11 (6), location 33×110.2 (Ref. 31.7×116.9).



FELIX and BURBRIDGE, Carboniferous miospores (Springer fm)

sculptured with muri 3–5 μ wide and up to 3.5 μ high, enclosing lumina ranging from $2 \times 3.5 \mu$ to $5.5 \times 7 \mu$. Wall distinct, 15 μ wide including muri.

Discussion. The meshlike network of the reticulum appears to be more comparable to wall features described for *Reticulatasporites*, rather than the enclosing reticulum characteristic of *Dictyotriteles* and *Reticulatisporites*. The occasional peltate muri terminations are similar to those in *Reticulatisporites peltatus* and *Raistrickia boleta* to a limited degree, but these forms do possess a loosely enclosing reticulum. *Retialetes* of Staplin (1960) is alete but is ellipsoidal, generally ruptured, and with a finer reticulum without the exceedingly thickened exine. *Maculatasporites* (Tiwari 1964) seems to be comparable to *R. lacunosus* in features of reticulum and exine, although its size range is considerably smaller. However, age difference of sediments is great enough to warrant questioning such a comparison, and Tiwari's differentiation from *Reticulatasporites* on muri features does not seem justified in our opinion.

Subturma PERINOTRILETES Erdtman 1947

Genus PEROTRILITES (Erdtman) ex Couper 1953

Type species. *P. granulatus* Couper 1953.

Perotrilites perinatus Hughes and Playford 1961

Plate 57, figs. 14, 15

Description. Radial, trilete, circular. Perispore thin, hyaline, loose about spore body and extending beyond the spore margin 1.5–3 μ . Elements of reticulum not exceeding 1 μ in width.

Dimensions. (25 specimens.) Diameter 42–65 μ .

Discussion. The sporotype was suggested by Erdtman (1947) for fossil trilete spores, less than 200 μ , with a distinct perine or perispodium. Although a form genus and established by Couper for Jurassic spores, Hughes and Playford (1961) made use of it for their assignment of lower Carboniferous spores. Jansonius (1962) suggested *P. perinatus* to be synonymous with *Proprisporites rugosus*. This seems to be a rather vague comparison and without reliable evidence.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Genus VELAMISPORITES Bhardwaj and Venkatachala 1962

Type species. *V. rugosus* Bhardwaj and Venkatachala 1962.

Discussion. Well-preserved, entire specimens of this genus bear a superficial resemblance to *Convolutispora*. However, the sculpture of *Convolutispora* consists of anastomosing rugulae which are a part of the exine, whereas in *Velamisporites* the convolutions are a feature of the perispore membrane. Due to the loosely enveloping perispore and its characteristic of fragmenting off, the true diameter is often difficult to ascertain. However, the holotype of *V. vermiculatus* (Pl. 59, fig. 1) probably represents an intact specimen. Small specimens such as *V. discretus* (Pl. 59, fig. 3) possibly illustrate a collapsed perispore from which the body has been lost. There is a sizeable variation in

the included spore bodies, but they are numerous and the clinging remnants of the membrane and its characteristic convolutions renders identification easy.

Velamispores descretus Bhardwaj and Venkatachala 1962

Plate 59, figs. 2, 3

Dimensions. (10 specimens.) Equatorial diameter (including perispore) 75–125 μ .

Discussion. This species is relatively rare in the Springer formation. Bhardwaj and Venkatachala (1962) gave a size of 90–110 μ in the original diagnosis. Other than the difference in size range, the Springer specimens compare with their description in all respects. Spore type 4 of Love (1960) is probably this species with much of its perispore membrane removed.

Velamispores vermiculatus sp. nov.

Plate 59, fig. 1

Diagnosis. Spore circular, trilete, covered with dense, perispore membrane which is heavily ornamented with vermiculate thickenings of variable width and length. Spore body wall 2–4 μ thick and laevigate. Laesurae difficult to discern due to perispore but is about two-thirds distance of radius, with little lip development, and without visible commissures. Perispore membrane generally laevigate although rare specimens possess some granulose ornamentation; convolutions show no regular pattern of development, often intertwining and infrequently forming loosely knit reticulations; convolutions range in width from 2–10 μ (4–6 μ , median).

Dimensions. (25 specimens.) Equatorial diameter (including perispore) 115–200 μ . Spore body 65–140 μ .

Holotype. Slide O3V16–5 (1). Location 9·8 × 107·3 (Ref. 32·5 × 118).

Description. Holotype circular, 180 × 190 μ in diameter. Central body obscured by perispore, trilete indistinct. Laevigate perispore covered with thick irregular convolutions 8–10 μ in width; the rope-like convolutions measure up to 65 μ in length without divisions, but an accurate determination of length is difficult.

Comparison. There is a similarity to *V. rugosus* Bhardwaj and Venkatachala 1962. However, that species possesses a definite and uniform granulose perispore covering. The perispore in *V. vermiculatus* encloses the spore body more loosely, and the thickened, vermiculate convolutions are decidedly larger and more pronounced. The authors have observed specimens of *V. rugosus* in Caney age strata of Oklahoma, and the distinction between the two species is readily apparent.

Other occurrences. Subsurface Springer formation of the Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; New Livingston Coal, Gizzard formation, lower Pennsylvanian, Rockcastle County, Kentucky; subsurface Hartselle formation, upper Mississippian, Warrior Basin, Alabama. In addition, *V. rugosus* has been observed from the surface Caney formation, upper Mississippian, Johnston County, Oklahoma.

Turma ZONALES (Bennie and Kidston) R. Potonié 1956

Subturma AURITOTRILETES Potonié and Kremp 1954

Infraturma AURICULATI (Schopf 1938) Potonié and Kremp 1954

Genus TRIPARTITES Schemel 1950

Type species. T. vetustus Schemel 1950.*Tripartites dubitalis* sp. nov.

Plate 58, figs. 3, 4

Diagnosis. Radial, trilete. Laesurae simple, 12–14 μ long, extending to at least four-fifths body radius. Body punctate proximally and distally; proximal surface marked by rows of coarser punctations bordering laesurae. Outline subtriangular with concave sides and apices with dark, well-defined auriculae. Auriculae appear solid in well preserved specimens, not connected interradially. Auriculae extend 6–11 μ beyond apices, plicated or fluted in weathered specimens, with blunt spines projecting up to 3.5 μ .

Dimensions. (10 specimens.) Equatorial diameter 43–49 μ . Spore body diameter 27–32 μ .

Holotype. Slide O3V17–1 (5). Location 44.8 $\times$ 127.8 (Ref. 32 $\times$ 119).

Description. Holotype 45 $\times$ 45 μ , body 27 $\times$ 27.5 μ . Auriculae extending 9–11 μ beyond apices, slightly fluted and projecting rodlets faintly visible. Laesurae 12 μ long, about four-fifths body radius. Wall punctate proximally and distally, punctations dense along laesurae.

Comparison. This species does resemble *T. vetustus* and is within the prescribed size limits as recognized in the Springer. However, the narrow, almost solid auriculae are distinctive, and the punctations of the spore wall are a constant feature in *T. dubitalis* but not of *T. vetustus*. The markedly coarser rows of punctations along the laesurae are also unique for this species.

Tripartites vetustus Schemel 1950

Plate 58, fig. 5

Description. Radial, trilete. Laesurae simple, length 10–14 μ or two-thirds to three-fourths body radius. Body usually laevigate but sometimes minutely punctate, outline subtriangular with concave sides. Prominent auriculae extend beyond apices 10–13 μ , not connected interradially. Radial portion of auriculae usually fluted or lobed, sometimes appear entire but outer portion usually membranous; in weathered or over-macerated specimens five to six blunt processes are visible.

Dimensions. (25 specimens.) Equatorial diameter 48–60 μ . Spore body diameter 29–34 μ .

Discussion. The described size range of *T. vetustus* is 30–40 μ , but this is the sole difference between the Springer forms and previously described occurrences. In view of the impossibility of making a distinction on any feature other than size, it is felt that they are conspecific and represent an extension of the size limits.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus AHRENSISPORITES Potonié and Kremp 1954

Type species. *A. guerickei* (Horst) Potonié and Kremp 1954.

Alrensisporites irroratus sp. nov.

Plate 58, fig. 6

Diagnosis. Radial, trilete, outline triangular. Sides straight or slightly convex. Laesurae simple, extending nearly to body margin. Prominent distal kyrtole nearly continuous. Apical auriculae $6 \times 15 \mu$ to $8 \times 30 \mu$. Body ornamented proximally and distally with rounded granules $1-2 \mu$ in diameter and 1μ in height.

Dimensions. (10 specimens.) Equatorial diameter $40-60 \mu$.

Holotype. Slide O3V17-1 (3). Location 34.5×112 (Ref. 31×119.5).

Description. Holotype $44 \times 45 \mu$. Auriculae $6 \times 15 \mu$ to $7.5 \times 19 \mu$. Laesurae simple, $18-19 \mu$ long, extending nearly to body margin. Distal kyrtole 6μ in height, nearly continuous, extending 38μ in longest dimension. Granulations 1μ in height and average 1.5μ in diameter; situated $1-2 \mu$ apart.

Discussion. In a few specimens the concentration of granulations appeared to be slightly more dense along the rays, but this was not a consistent feature. Among previously described species, *A. beeleyensis* Neves 1961 is of similar size but has kyrtoles of blunt cones forming a dentate structure, while *A. guerickei* var. *ornatus* Neves 1961 is considerably larger and ornamented with irregular, wart-like thickenings. Horst's (1955) fig. 61 of *A. guerickei* resembles *A. irroratus* in ornamentation. However, in his specific diagnosis Horst specifies a 'smooth' body for *A. guerickei*.

Genus SCUTULUM gen. nov.

Type species. *S. pusillum* sp. nov.

Diagnosis. Radial, trilete, convexly subtriangular, laevigate. Bearing subtriangular to rounded platelet on the proximal surface; platelet with three radiating arms or projections, terminating at the apices. Laesurae distinct, oriented on the proximal platelet, extending three-fourths to two-thirds distance of spore radius. Distal surface unornamented. Spore wall thin.

Scutulum pusillum sp. nov.

Plate 58, fig. 7

Diagnosis. Radial, trilete; convexly subtriangular, laevigate. Proximal side bearing subtriangular to rounded platelet with projecting arms terminating at apices. Trilete oriented on the central platelet with laesurae concurrent with platelet arms. Platelet dimensions $16-27 \mu$; radiating arms $5-10 \mu$ long, $4-7 \mu$ in width. Laesurae $11-15 \mu$ long, extending three-fifths to two-thirds distance of spore radius. Commissure distinct, slight lip development. Distal side unornamented. Spore wall thin, not exceeding 1μ .

Dimensions. (6 specimens.) Equatorial diameter $31-47 \mu$.

Holotype. Slide O3V16-9 (A-1). Location 27.5×112 (Ref. 31×116.5).

Description. Holotype subtriangular with slightly convex margins and rounded apices. Over-all diameter $31.5 \times 34.5 \mu$; central platelet $16 \times 19 \mu$, radiating arms 4–5 μ wide and 9–10 μ long. Laesurae prominent, 9.5–12 μ long, three-fifths of the spore radius.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma. The only additional record of this spore known to the authors is from the subsurface Mississippian Chainman formation in the Standard Continental Hayden Creek Unit No. 1 well, White Pine County, Nevada. The authors are indebted to Mr. Virgil D. Wiggins for this material, which was used by Wiggins for his prize-winning 1960 AAPG–SEPM contribution (Wiggins 1961).

Genus TANTILLUS gen. nov.

Type species. *T. triquetrus* sp. nov.

Diagnosis. Radial, trilete, triangular with concave sides, laevigate to granulose. Laesurae simple, not always visible, extending two-thirds of spore radius. Radial extremities rounded to gently pointed. Triangular thickening on distal side more concave than spore body. It expands at its apices forming shoulders which spread to equal the width of the body. This thickening is the identifying characteristic of the genus and is often developed to different degrees at the various apices on a single specimen. The apices of the spore body extend past the apices of the distal thickening and give the impression of swollen auriculae. Spore wall very thin.

Tantillus triquetrus sp. nov.

Plate 65, figs. 4, 5

Diagnosis. Radial, trilete, triangular with concave sides, laevigate to minutely granulose. Laesurae 9–12 μ long extending two-thirds spore radius. Radial extremities rounded to gently pointed. Triangular thickening on the distal side more concave than spore body, forming apical shoulders which spread to equal the width of the body. Shoulders are 4–13 μ across and terminate in a peltate, paterate, or T-shaped manner, often displaying this variety on a single specimen.

Dimensions. (35 specimens.) Equatorial diameter 16.5–25 μ .

Holotype. Slide O3V16–11 (6). Location 40.8 $\times$ 110.1 (Ref. 31.7 $\times$ 116.9).

Description. Holotype 18 $\times$ 18 μ , radial, trilete, triangular with concave sides, laevigate. Laesurae 9 μ long, extending two-thirds distance of spore body radius. Radial extremities rounded. The distal thickening expands to 9 μ across with one paterate and two T-shaped apices. Spore wall very thin.

Discussion. The genus bears a resemblance to *Stellisporites* Alpern, Girardeau and Trolard 1958, but their genus evidently did not possess the distal thickening or the distinctive apical terminations.

Other occurrences. Subsurface Springer formation of the Anadarko Basin, blue shale above Lily Coal, Breathitt formation, Whitley County, Kentucky; Barnsley Coal,

southern Pennines, England. The Barnsley Coal is an exchange sample received from Dr. Roger Neves; the Barnsley Coal and the Kentucky blue shale are both Westphalian B age.

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI (Potonié and Klaus) Dettmann 1963

Genus LYCOSPORA (Schopf, Wilson, and Bental) Potonié and Kremp 1954

Type species. *L. micropapillata* (Wilson and Coe) Schopf, Wilson, and Bental 1944.

Lycospora brevijuga Kosanke 1950

Plate 58, fig. 8

- 1950 *Lycospora brevijuga* Kosanke, p. 44, pl. 10, fig. 5.
- 1957 *Lycospora subjuga* Bhardwaj, p. 127, pl. 25, figs. 84–86.
- 1962 *Lycospora brevijuga* Kosanke; Piérart, p. 104, pl. F, figs. 32–34.

Description. Radial, trilete, subtriangular. Laesurae straight, distinct, extending to body margin; very slight lip development, commissures distinct. Body minutely punctate, with scattered apical papillae. Very small flange development, not exceeding $1\ \mu$ in width.

Dimensions. (20 specimens.) Over-all equatorial diameter 25–40 μ .

Lycospora nitida (Horst) Potonié and Kremp 1955

Plate 58, figs. 9, 10

- 1955 *Lycospora nitida* (Horst) Potonié and Kremp in Horst p. 181, pl. 24, fig. 81.
- 1956 *Lycospora* (*Triletes*) *nitida* (Horst) Potonié and Kremp; Potonié and Kremp, p. 101.
- 1957 *Simozonotriletes trilinearis* Artüz; Artüz p. 251, pl. 5, fig. 36 *a, b*.
- 1957 *Bellisporos bellus* Artüz; Artüz p. 255, pl. 7, fig. 49 *a, b*.
- 1958 *Lycospora nitida* (Horst) Potonié and Kremp; Butterworth and Williams, p. 375, pl. 3, fig. 9.
- 1959 *Simozonotriletes trilinearis* Artüz; Artüz, p. 46, pl. 8, fig. 51 *a, b*.
- 1959 *Bellisporos bellus* Artüz; Artüz p. 52, pl. 10, fig. 64 *a, b*.
- 1962 *Bellisporos*; Venkatachala and Beju p. 146, pl. 2, figs. 5–7.

Description. Radial, subtriangular to triangular, margins linear to concave; equatorial flange moderate to strongly dentate and about $4\ \mu$ wide. Trilete, laesurae extend to margin of body, lips distinct and $3\text{--}7\ \mu$ wide; wall thickness $1\ \mu$, minutely reticulate proximally and distally.

Dimensions. (25 specimens.) Over-all equatorial diameter 30–42 μ .

Discussion. Artüz's (1957) establishment of *Lycospora nitida* is invalid, being a later homonym, since Horst (1955) had legitimately applied the name to a morphologically different spore. In addition, Artüz's (1957) application of *L. nitida* was to a spore which appears to be most nearly comparable to *L. noctuina* (*sensu* Butterworth and Williams). On the other hand, her *Bellisporos* is rather obviously conspecific with *Lycospora nitida* Horst 1955. Similarly, Venkatachala and Beju (1962, p. 147) also overlooked or ignored Horst's earlier treatment when they identified *Bellisporos*. In a more recent publication Sullivan (1964a) has described *B. bellus*, distinguishing it from *L. nitida* by the greater

concavity of the radial thickenings. However, such a variety of these thickenings appear to be present in the Springer specimens that any such differentiation is impossible.

It is debatable whether this spore actually belongs in *Lycospora*, and Butterworth and Williams (1958) earlier expressed their doubts. It does differ, especially in its labial structure, from the known species definitely associated with the arborescent lycopods. However, much is still unknown about lycopod spore associations and Potonié and Kremp (1956a) did include *L. nitida* within the emended generic framework. Though the generic designation may seem inappropriate, its rejection is not advisable until more light can be shed on the spore's affinity.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; Game Refuge Sandstone, upper Jackfork formation, Le Flore County, Oklahoma.

Lycospora noctuina Butterworth and Williams 1958

Plate 58, figs. 11, 12

1957 *Lycospora nitida* Artüz; Artüz p. 250, pl. 5, fig. 34 a, b.

1958 *Lycospora noctuina* Butterworth and Williams, p. 376, pl. 3, figs. 14, 15.

1959 *Lycospora nitida* Artüz; Artüz p. 45, pl. 7, fig. 48 a, b.

Description. Radial, trilete, convexly subtriangular. Laesurae distinct, straight, length equal to body radius; distinct lips 1.5–2 μ in width. Cingulum 3–7 μ wide, two zones often evident with inner area solid and outer zone membranous and with minute perforations often present. Central body ornamented with prominent projections of varying sizes and shapes, ranging from large granules to obervermiculate ridges.

Dimensions. (50 specimens.) Over-all diameter 30–40 μ .

Discussion. Butterworth and Williams (1958) noted that the cingulum width roughly equals the radius of the central area. In the Springer specimens the cingulum width more nearly attains about one-half the radius of the spore body, and this actually appears to be the case with specimens figured in the original description by Butterworth and Williams (pl. 3, figs. 14, 15). Our specimens also display a distinct undulation of the outer edge of the cingulum, which seems to be characteristic. There is also considerable variation in the shape and the distribution of the wall ornamentation, which is the chief distinguishing feature of the species. It varies from granules of 1 μ in diameter to oval and rectangular prominences of 4–5 μ dimensions. The obervermiculate ridges are 1–3.5 μ in width and of varying lengths. We have observed them in patterns such as 3.5 $\times$ 6.5 μ , 1.5 $\times$ 8.5 μ , 2 $\times$ 9 μ , and 1.5 $\times$ 15 μ . Specimens may range from those with little degree of vermiculation to almost dense convolutions, and it was also observed that when there was a difference in distal and proximal ornamentation, the greater degree of ornamentation and vermiculation occurred on the distal surface. This spore is almost certainly the same one that Artüz (1957, 1959) assigned to *L. nitida*. It is quite probable that her *Lycospora paulula* is synonymous with *L. noctuina*. In any case her assignment is not valid as pointed out in our treatment of *L. nitida*. *L. noctuina* is one of the more numerous and easily recognized entities occurring in the Springer assemblages, and it is especially noteworthy in samples O3V16–4 and O3V16–9.

Other occurrences. Subsurface Springer formation, Anadarko Basin; subsurface Chester formation, upper Mississippian, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; surface Prairie Mountain and Wildhorse Mountain formations, Jackfork group, Ouachita Mts., Oklahoma; Livingston Coal, Gizzard formation, Rockcastle County, Kentucky; Stearns #1 Coal, Gizzard formation, McCreary County, Kentucky.

Lycospora pseudoannulata Kosanke 1950

Plate 58, fig. 13

- 1950 *Lycospora pseudoannulata* Kosanke, p. 45, pl. 10, fig. 7.
 1955 *Cirratiradites pseudoannulatus* (Kosanke) Hoffmeister, Staplin, and Malloy, p. 383, pl. 36, fig. 25.
 1956 *Lycospora pseudoannulata* Kosanke; Potonié and Kremp, p. 103, pl. 17, figs. 345, 346.

Description. Radial, trilete, subtriangular. Laesurae distinct, straight, length equal to body radius, lips and commissure prominent. Body granulose, wall 2 μ thick. Cingulum up to 5 μ in width, laevigate, with numerous perforations.

Dimensions. (25 specimens.) Equatorial diameter 30–37 μ .

Lycospora uber (Hoffmeister, Staplin, and Malloy) Staplin 1960

Plate 58, fig. 14

- 1955 *Cirratiradites uber* Hoffmeister, Staplin, and Malloy, p. 383, pl. 36, fig. 24.
 1957 *Cirratiradites uber* Hoffmeister, Staplin, and Malloy; Hacquebard and Barss, p. 39, pl. 5, fig. 11.
 1960 *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin, p. 20, pl. 4, figs. 13, 17, 18, 20.
 1963 *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin; Playford, p. 636, pl. 89, figs. 16, 17.

Description. Radial, trilete, convexly subtriangular. Laesurae straight, distinct, extending to body margin, lips prominent. Body finely granulose to slightly verrucose. Flange 2–5 μ in width, laevigate, usually perforated and ragged in appearance.

Dimensions. (25 specimens.) Equatorial diameter 32–42 μ .

Genus ROTASPORA Schemel 1950

Type species. *R. fracta* Schemel 1950.

Rotaspora fracta Schemel 1950

Plate 58, fig. 15, 16

Description. Radial, trilete; body subtriangular with interrarial margins concave. Cingulum 5–7.5 μ wide interradi ally and 1–2 μ wide at apices; thickened at periphery to form narrow rim. Laesurae extending nearly to body margin, 12–15 μ long; commissure distinct, lips narrow, not exceeding 1 μ in width. Surface laevigate.

Dimensions. (25 specimens.) Over-all diameter 28–35 μ . Body diameter 25–33 μ .

Discussion. The Springer specimens agree with previous descriptions of the species in all details except cingulum width, where it exceeds most published measurements. However, Butterworth and Williams (1958, fig. 19) indicate an interrarial width of about $7\ \mu$, which compares with the Springer spores.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

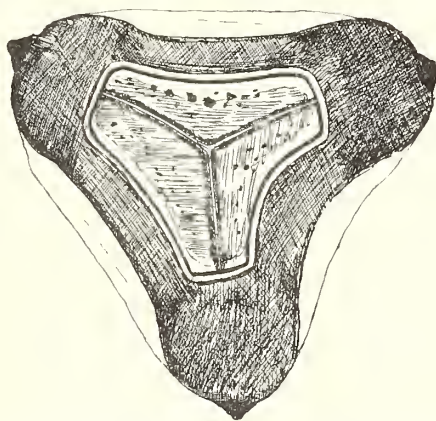
Genus SIMOZONOTRILETES Potonié and Kremp 1954

Type species. *S. intortus* (Waltz) Potonié and Kremp 1954.

Simozonotriletes intortus var. *polymorphosus* Sullivan 1958

Plate 58, fig. 17; text-fig. 3

Description. Spores triangular in equatorial plane with sides straight to slightly concave. Apices rounded, thickened, sometimes terminating in minute bosses. Cingulum continuous along sides in interrarial region and differentiated into two zones; inner zone dark, thickened, $3\text{--}5\ \mu$ wide, expanding at the apices into pad-like valvae; outer zone light, membranous in appearance, $2\text{--}3\ \mu$ in width, restricted largely to interrarial region and usually not projecting beyond the apical valvae, rarely the outer zone will encircle the valvae to a width not exceeding $1\ \mu$. Laesurae distinct, length exceeding three-fourths of spore radius, well-developed lips $1.5\ \mu$ wide. Body wall $1\ \mu$ wide, laevigate to finely punctate, punctations usually restricted to outer margin of laesurae.



Dimensions. (20 specimens.) Equatorial diameter $30\text{--}42\ \mu$. Body proper $18\text{--}24\ \mu$ in diameter.

TEXT-FIG. 3. *Simozonotriletes intortus* var. *polymorphosus* Sullivan 1958. Proximal surface; slide O3V16-11 (6), location 54.5×125 (Ref. 31.7×116.9).

Discussion. The minute projections of the apices do not exceed $2\ \mu$ in length and are not a consistent feature. Very few specimens were observed with all three valvae so ornamented, and perhaps one-half of the specimens observed did not possess them at all. Sullivan (1958) has illustrated a wide variation of differences in *Simozonotriletes*. These would ordinarily result in separation into different genera, were it not for his demonstrating such a continuity in variational patterns that it is impossible to even differentiate species. He noted several infraspecific categories, which possessed an interrarial cingulum of two zones. In each instance the bizonate cingulum consisted of an outer dark and an inner light zone. The occurrence of the outer light zone in the Springer specimens is the only significant difference from Sullivan's observations. He established *S. intortus* var. *polymorphosus* to include a very wide variation. Even though the Springer specimens are considerably smaller than the limits he assigned and the cingulum zonation differs, assignment appears most practical since the diversity of morphological types

Sullivan demonstrated for the genus does not allow for confident assignment to new taxon status on the basis of so few dissimilarities.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Genus *DENSOSPORITES* (Berry) Butterworth, Jansonius, Smith, and Staplin 1964

Type species. *D. covensis* Berry 1937.

Remarks. The morphologic spore types included within the 'densosporites' contain a number of perplexing problems. Playford (1962) recognized *Anulatisporites* as distinct from *Densosporites*, but he seemed to base much of his opinion on the uncompleted appraisal the densosporites were receiving by the International Commission for the Microflora of the Palaeozoic. The subsequent opinion of the C.I.M.P. working group No. 2 (Butterworth *et al.* 1964) and of Staplin and Jansonius (1964) resulted in an emendation of *Densosporites* and rejection of *Anulatisporites*. This interpretation is accepted and is utilized in the assignment of *Densosporites velatus* sp. nov.

Densosporites velatus sp. nov.

Plate 59, figs. 4, 5

Diagnosis. Spores radial, subtriangular to circular. Laesurae distinct, straight, extending three-fourths of body radius; commissure distinct, very slight lip development. Body minutely granulose proximally and distally at high magnification. Cingulum undifferentiated, laevigate. Spore originally enclosed within perispore membrane, fragments of the perispore adhering to specimens.

Dimensions. (25 specimens.) Over-all diameter 65–75 μ . Diameter of body 36–50 μ . Cingulum 8–16 μ wide.

EXPLANATION OF PLATE 59

All figures $\times 500$ unless otherwise indicated.

Fig. 1. *Velamispores vermiculatus* sp. nov. Holotype. Slide O3V16–5 (1), location 9.8 $\times$ 107.3 (Ref. 32.5 $\times$ 118).

Figs. 2, 3. *Velamispores discretus* Bhardwaj and Venkatachala 1962. 2, Slide O3V16–10 (B-2), location 13 $\times$ 107.5 (Ref. 32 $\times$ 117.3). 3, Perispore; Slide O3V16–5 (1), location 43.4 $\times$ 107 (Ref. 32.5 $\times$ 118).

Figs. 4, 5. *Densosporites velatus* sp. nov. 4, Holotype. Proximal surface; Slide O3V17–2 (1), location 48 $\times$ 115.9 (Ref. 31 $\times$ 117.9). 5, With perispore; Slide O3V17–1 (4), location 19.5 $\times$ 115 (Ref. 32 $\times$ 119.6).

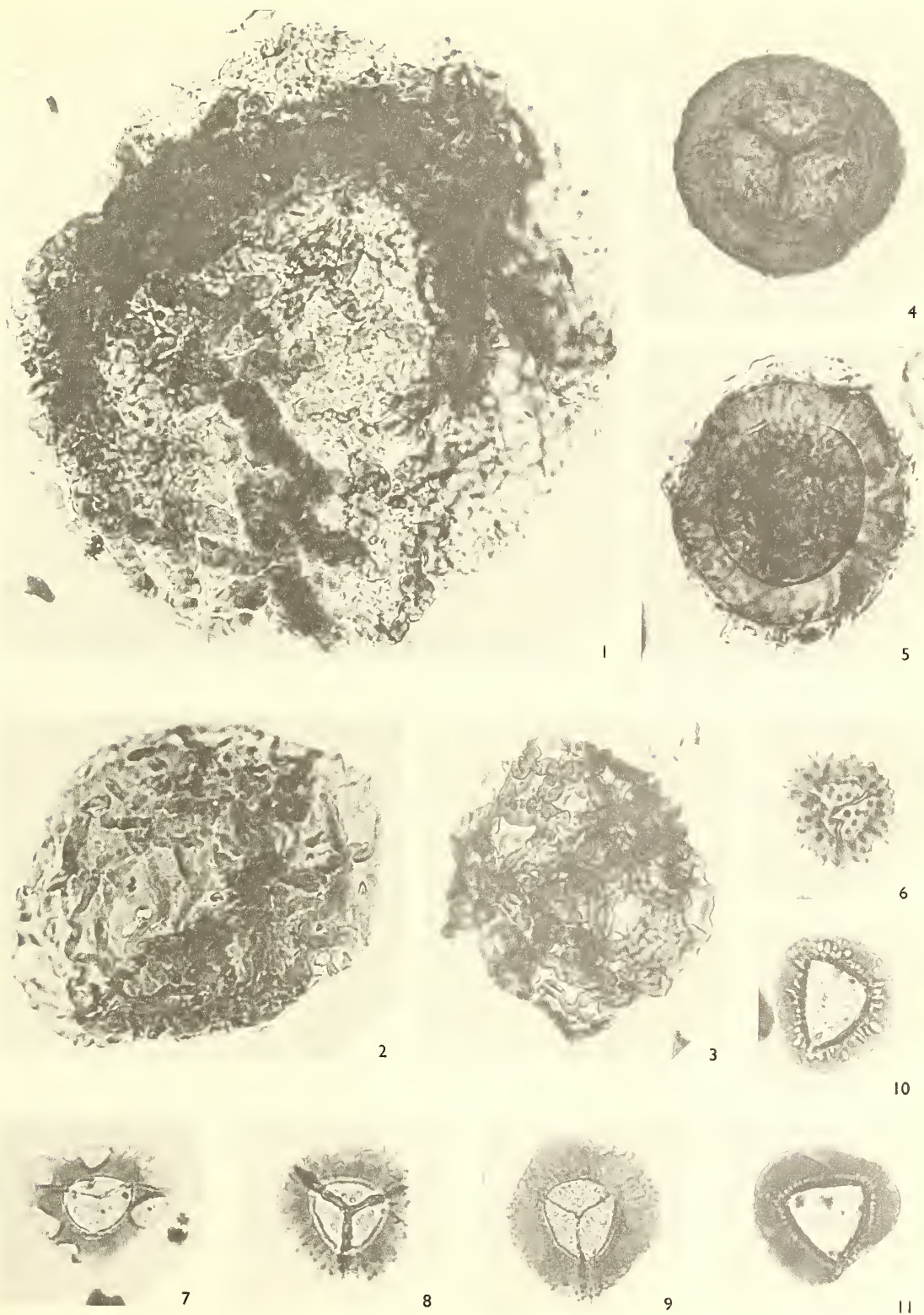
Fig. 6. *Densosporites aculeatus* Playford 1963. Proximal surface; Slide O3V16–3 (1), location 25 $\times$ 113 (Ref. 33 $\times$ 117.1).

Fig. 7. *Densosporites irregularis* Hacquebard and Barss 1957. Proximal surface; Slide O3V16–13 (A-1), location 50.4 $\times$ 109.5 (Ref. 31.1 $\times$ 117.9).

Fig. 8. *Densosporites rarispinosus* Playford 1963. Proximal surface; Slide O3V16–3 (6), location 18.8 $\times$ 125.1 (Ref. 33 $\times$ 117.9).

Fig. 9. *Densosporites hispidus* sp. nov. Holotype. Proximal surface; Slide O3V17–1 (4), location 11 $\times$ 114.4 (Ref. 32 $\times$ 119.6).

Figs. 10, 11. *Densosporites variabilis* (Waltz) Potonié and Kremp 1956. 10, Showing pyriform pits; Slide O3V16–13 (6), location 47 $\times$ 121.5 (Ref. 32.8 $\times$ 119.5). 11, Slide O3V16–14 (5), location 29 $\times$ 113.5 (Ref. 32.3 $\times$ 117.6).



Holotype. Slide O3V17-2 (1). Location 48×115.9 (Ref. 31×117.9).

Description. Holotype $65 \times 70 \mu$ over-all. Body diameter $36 \times 40 \mu$. Cingulum $14-16 \mu$ wide, laesurae extending four-fifths distance of body radius, commissure distinct, lips narrow; perispore remnants forming reticulum over entire specimen.

Discussion. The presence of a perispore or perine in mature spores is characteristic of a number of species. It is admittedly questionable as a safe criterion for comparative purposes due to uncertainty of its presence in some genera, while closely related representatives may possess it; it may be a feature present only at maturity, and in fossil ferns the structure may be lost in preservation or through maceration. In *D. velatus* a thick perispore must have been present at maturity, and some specimens possess a membranaceous sheath extending as much as 15μ beyond the spore's margin (Pl. 59, fig. 5). The enclosing perispore consists of a loosely reticulate structure, the elements being $1-2 \mu$ in thickness. Portions of this reticulum are always present, even though the membrane may be absent. It is conjectural whether the species could be identified without any of the perispore remaining. However, the species is abundant in this study and scores of specimens observed, but at no time were representatives encountered which appeared to be *D. velatus* without the perispore.

Densosporites aculeatus Playford 1963

Plate 59, fig. 6

Description. Radial, trilete; equatorial margin and distal surface bearing simple spines, rounded at base, with basal diameter $2-3.5 \mu$; length $2-4.5 \mu$. Laesurae straight to sinuous, frequently extending slightly beyond body margin; rays $10-15 \mu$ in length, commissure distinct and lips up to 2μ in height on well preserved specimens. Spore body laevigate and wall 1.5μ thick.

Dimensions. (25 specimens.) Equatorial diameter, exclusive of spinose projections, $35-45 \mu$. Body $17-22.5 \mu$ in diameter.

Discussion. The Springer specimens are in the lower limits of Playford's (1963) size range, but agreement is very close on every morphological detail.

Other occurrences. Surface Goddard formation, upper Mississippian.

Densosporites hispidus sp. nov.

Plate 59, fig. 9

Diagnosis. Radial, trilete, roundly subtriangular. Laesurae distinct, simple, usually straight but sometimes slightly sinuous; $10-14 \mu$ long, usually extending only to body margin, occasionally extending on to cingulum. Body laevigate proximally; distal surface conspicuously ornamented with small granules approximately 1μ in diameter and spaced 1μ apart. Cingulum of uniform width, $10-17 \mu$ wide, laevigate proximally; distal surface with minute spines projecting; spines acute, seldom exceeding 1μ in length, and spaced $1-2 \mu$ apart; on corroded specimens the cingulum spines are more prominent and visible about outer periphery of spore.

Dimensions. (25 specimens.) Over-all diameter 41–60 μ . Body 20–29 μ in diameter.

Holotype. Slide O3V17–1 (4). Location 11 $\times$ 114.4 (Ref. 32 $\times$ 119.6).

Description. Holotype convexly subtriangular. Over-all diameter 49 $\times$ 51.5 μ ; body 20 $\times$ 29 μ . Laesurae 12–13 μ long, slightly sinuous, extending slightly on to cingulum, commissure not visible. Cingulum 13–15 μ wide, uniform; laevigate proximally and with numerous minute spines projecting from the distal surface. Body laevigate proximally and with numerous, closely spaced granules on distal surface.

Discussion. The cingulum in *D. hispidus* is very uniform and shows little tendency to break down into more than one zone as is characteristic of several species of the genus. There does not appear to be any internal system of struts or bars, and the minute spines of the distal side are the only ornamentation features. They present a bristle-like appearance and are readily discernible only at high magnifications.

Comparison. *D. hispidus* shows some resemblance to a number of previously described species but cannot be properly assigned to any of these. *D. spitsbergensis* (Playford 1963) has spines on the distal body surface rather than granules, and they are quite large, being 1.5–5 μ in length. *D. rarispinosus* (Playford 1963) has a conspicuous distal sculpture of sizeable spines and small verrucae. *D. spinosus* of Dybová and Jachowicz (1957) is described as being spinose distally and granulose proximally. *D. faunus* Ibrahim as figured by Dybová and Jachowicz (pl. 52, figs. 1, 2) bears some resemblance to *D. hispidus*, but their description makes no mention of ornamentation types or distribution other than being rugose. *D. spongeosus* Butterworth and Williams (1958, p. 380) has a body with typically minute perforations and sometimes granular or finely vermiculate. This species has subsequently been reduced to synonymy with *D. triangularis* Kosanke by Butterworth *et al.* (1964).

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Densosporites irregularis Hacquebard and Barss 1957

Plate 59, fig. 7

Diagnosis. Radial, trilete, rays usually difficult to discern but visible on well-preserved specimens, reaching to body margin. Cingulum thick and opaque adjacent to spore body, becoming translucent and membranous towards the periphery; opaque portion lobed and extending toward the outer margin of the cingulum in the manner of wheel spokes.

Dimensions. (20 specimens.) Over-all diameter 40–48 μ . Body 20–24 μ in diameter.

Discussion. Except for size, the Springer material compares with the species description of Hacquebard and Barss (1957). The Springer spores are smaller than the range of 58–75 μ given for the species. Variations do exist in the arrangement of the opaque portion of the cingulum, but preservation and maceration appear to be responsible.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard

formation, upper Mississippian, Johnston County, Oklahoma; Livingston Coal, Gizzard formation, Rock Castle County, Kentucky; Stearns #1 Coal, Gizzard formation, McCreary County, Kentucky.

Densosporites rarispinosus Playford 1963

Plate 59, fig. 8

Diagnosis. Radial, trilete. Laesurae distinct, sinuous, extending beyond the body margin; commissure distinct and prominent lips up to $2.5\ \mu$ in height. Distal surface of body and cingulum bearing sparsely distributed simple spines, which project slightly from the equatorial margin (up to $3.5\ \mu$). Body spines average $1.5\ \mu$ in diameter and are scattered $1\text{--}3\ \mu$ apart. There are rare distal verrucae up to $2.5 \times 4.5\ \mu$. Body wall conspicuous, $1.5\ \mu$ thick.

Dimensions. (25 specimens.) Equatorial diameter, exclusive of spinose projections, $40\text{--}50\ \mu$. Body $20\text{--}23\ \mu$ in diameter.

Discussion. It is best distinguished from the closely allied *D. aculeatus* by the more prominent laesurae. The laesurae appear to always extend well beyond the body margin, frequently entirely across the cingulum. In *D. aculeatus* this extension beyond the body margin is not a regular feature. The spinose distal sculpture is much more conspicuous in *D. aculeatus*.

Densosporites variabilis (Waltz) Potonié and Kremp 1956

Plate 59, figs. 10, 11

- 1938 *Zonotriletes variabilis* Waltz in Luber and Waltz, pp. 20–21, pl. 4, figs. 44–46, and pl. A, fig. 16.
- 1941 *Zonotriletes variabilis* Waltz var. *foveolatus* Waltz in Luber and Waltz, p. 26, pl. 5, fig. 66a.
- 1941 *Zonotriletes variabilis* Waltz var. *fossulatus* Waltz in Luber and Waltz, p. 26, pl. 5, fig. 66b.
- 1941 *Zonotriletes variabilis* Waltz var. *valleculosus* Waltz in Luber and Waltz, p. 27, pl. 5, fig. 66c.
- 1956 *Densosporites variabilis* (Waltz) Potonié and Kremp, p. 116.
- 1956 *Trematozonotriletes variabilis* (Waltz) Ishchenko var. *foveolatus* Waltz; Ishchenko, pp. 102–3, pl. 22, fig. 248.
- 1963 *Densosporites variabilis* (Waltz) Potonié and Kremp; Playford, pp. 625–6, pl. 88, figs. 19–22.

Description. Radial, trilete, subtriangular. Uniform cingulum $10\text{--}12\ \mu$ in width with ring of shallow, pyriform pits radially oriented about inner edge of cingulum; pits average $1.5\ \mu$ in longest dimension, rarely extend beyond centre of cingulum; occasional pit on outer edge and appears to be beginning point of corrosive deterioration of the cingulum; largest such pit noted measured $2.5\ \mu$ in width by $4\ \mu$ in length. The cingulum is thick and without any diagnostic interior features; in corroded or oxidized specimens cingulum breakdown does not reveal a system of supporting rodlets or struts such as occurs in many species. Laesurae indistinct, sinuous.

Dimensions. (25 specimens.) Over-all equatorial diameter $35\text{--}50\ \mu$. Body $21\text{--}25\ \mu$ in diameter.

Comparison. A row of pits near the inner margin of the equatorial portion is characteristic of *Vallatisporites*, and Hacquebard (1957) considered a marginal groove and single row of pits as sufficiently diagnostic to separate *Vallatisporites* from *Densosporites*. Although *Vallatisporites* is easily distinguished from *D. variabilis* on ornamentation and cingulum features, there is little difference in pit characters. This reflects some doubt on the accuracy of the pits as features of generic distinction. Similar pits have been noted in other *Densosporites* as corrosion products, but the well developed and uniform arrangement noted on even the best preserved specimens of *D. variabilis* from the Springer lends confidence in their taxonomic value.

Densosporites dissimilis sp. nov.

Plate 60, fig. 1

Diagnosis. Radial, trilete, subtriangular. Laesurae distinct, straight, simple with only slight lip development, extending to body margin. Body ornamented proximally with irregular granules up to $1 \times 3 \mu$ and distally with blunt con. Cingulum $13\text{--}17 \mu$ in width, consisting of an inner opaque zone $6\text{--}8.5 \mu$ in width and an outer translucent zone $6\text{--}10 \mu$ in width. Numerous blunt spines project from proximal and distal surfaces, being most conspicuous on weathered specimens. Body wall distinct, 1.5μ thick.

Dimensions. (10 specimens.) Over-all diameter $45\text{--}55 \mu$. Body $23\text{--}27 \mu$ in diameter.

Holotype. Slide O3V16-3 (6). Location 38×119.2 (Ref. 33×117.9).

Description. Holotype-subtriangular. Over-all diameter $53 \times 53 \mu$; body $25 \times 27 \mu$. Laesurae straight, 14μ in length, extending to body margin, commissure visible.

EXPLANATION OF PLATE 60

All figures $\times 500$ unless otherwise indicated.

Fig. 1. *Densosporites dissimilis* sp. nov. Holotype. Proximal surface; Slide O3V16-3 (6), location 38×119.2 (Ref. 33×117.9).

Fig. 2. *Knoxisorites corporeus* (Loose) Potonié and Kremp 1955. Distal surface; Slide O3V16-10 (A-1), location 15×119 (Ref. 29.5×118.2).

Fig. 3. *Knoxisorites dissidius* Neves 1961. Distal surface; Slide O3V16-13 (B-1), location 53.2×124 (Ref. 31.9×117.2).

Figs. 4, 5. *Knoxisorites hederatus* (Ishchenko) Playford 1963. 4, Distal surface; Slide O3V16-11 (6), location 46.8×116 (Ref. 31.7×116.9). 5, Proximal surface; Slide O3V16-11 (6), location 34×113.5 (Ref. 31.7×116.9).

Figs. 6, 7. *Knoxisorites triradiatus* Hoffmeister, Staplin, and Malloy 1955. 6, Proximal surface; Slide O3V16-3 (5), location 38×111.2 (Ref. 33.7×118). 7, Proximal surface; Slide O3V16-11 (7), location 25×115.7 (Ref. 31.9×117.9).

Figs. 8, 9. *Knoxisorites inconspicuus* sp. nov. 8, Distal surface; Slide O3V16-11 (7), location 29×122.1 (Ref. 31.9×117.9). 9, Holotype. Proximal surface; Slide O3V16-9 (A-1), location 47×125 (Ref. 31×116.5).

Figs. 10-14. *Knoxisorites stephanephorus* Love 1960. 10, Proximal surface; Slide O3V16-13 (A-2), location 51×122.3 (Ref. 32.2×117.9). 11, Distal surface; Slide O3V17-1 (5), location 39.5×114.2 (Ref. 32×119). 12, Proximal surface; Slide O3V16-11 (2), location 51.6×119.3 (Ref. 32×118). 13, Proximal surface; Slide O3V16-3 (1), location 34.8×120.1 (Ref. 33×117.1). 14, Proximal surface; Slide O3V16-9 (A-1), location 9.8×120 (Ref. 31×116.5).



Cingulum consisting of two sharply contrasting zones, an outer translucent area $6.5\text{--}8\ \mu$ wide and an inner opaque zone $7\text{--}8.5\ \mu$ wide; small blunt spines project from cingulum of weathered specimens. Proximal body surface ornamented with irregular granules, distal side with blunt con.

Comparison. A number of species have been described with a somewhat similar zonation of the cingulum, but *D. sphaerotriangularis* Kosanke 1950 is probably most closely comparable and differs largely only in ornamentation and ray features. *D. cuneiformis* Hacquebard 1957 has a like difference in ornamentation and rays, although comparable in size and cingulum morphology. The *Densosporites* figured by Venkatachala and Beju (1962, pl. 2, figs. 15, 17) appears comparable to *D. dissimilis*, but they do not provide any comparative data to accompany their illustrations.

Genus KNOXISPORITES (Potonié and Kremp) Neves 1961

Type species. *K. hageni* Potonié and Kremp 1954.

Knoxisporites corporeus (Loose) Potonié and Kremp 1955

Plate 60, fig. 2

1934 *Reticulatisporites corporeus* Loose, p. 155, pl. 7, fig. 7.

1955 *Knoxisporites corporeus* (Loose) Potonié and Kremp, p. 116, pl. 16, fig. 317.

Description. Radial, trilete, circular. Distinct cingulum not evident, although weakly defined one present occasionally. Laesurae straight, about $20\ \mu$ in length, two-thirds to three-fourths the spore radius, occasional rays extending nearly to margin. Lips $2\text{--}3\ \mu$ wide. Distal muri $4\text{--}7\ \mu$ wide.

Dimensions. (10 specimens.) Over-all diameter $60\text{--}90\ \mu$.

Discussion. Size range of the Springer specimens is greater than the maximum of $70\ \mu$ noted by Potonié and Kremp (1955), and the laesurae are slightly longer than in their description. The prominent lips were not commented on in the original description. This species was transferred to *Reticulatisporites* by Neves (1964) on the basis of possession of a differentially thickened cingulum. We have chosen retention in *Knoxisporites* and regard Neves's generic distinctions as insufficient. He has also retained *K. stephanophorus* in *Knoxisporites*, but we have observed in our study of this species a gradation from simple, non-zoned cingulum to a differentially thickened cingulum. Neves's treatment also leaves no repository for our species classified as *Reticulatisporites*. It appears that a much more thorough reappraisal of several cingulate genera is necessary before valid emendations may be made.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Knoxisporites dissidius Neves 1961

Plate 60, fig. 3

Description. Radial, trilete, outline rounded hexagonal. Distal surface with three radial bars uniting to enclose a triangular area at the distal pole. Laesurae three-fourths body radius. Exine laevigate.

Dimensions. (15 specimens.) Diameter 30–55 μ .

Discussion. The lower limits of the size are considerably below that reported by Neves (1961), who gave a size range of 50–80 μ . However, except for the generally smaller size, the spores correspond very well with Neves's description.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; subsurface Springer of the Anadarko Basin.

Knoxisporites hederatus (Ischenko) Playford 1963

Plate 60, figs. 4, 5

1956 *Euryzonotrites hederatus* Ischenko, pp. 58–59, pl. 10, fig. 121.

1963 *Knoxisporites hederatus* Ischenko; Playford, pp. 634–5, pl. 90, figs. 9–12; text-fig. 10a.

Description. Radial, trilete, circular to subcircular. Cingulum distinct, 6–12 μ wide. Laesurae simple, straight, 12–18 μ long and usually three-fourths of spore body radius, occasionally extending to body margin. Body distinct, exine laevigate. Muri sinuous, 4–12 μ wide, 3–6 μ high.

Dimensions. (25 specimens.) Over-all diameter 54–70 μ . Body diameter 42–50 μ .

Knoxisporites inconspicuus sp. nov.

Plate 60, figs. 8, 9

Diagnosis. Radial, trilete, subtriangular. Laesurae straight, three-fourths body radius, lips thin, about 1 μ in width, trilete fissures frequently gaped open. Spore subtriangular with convex sides, apices rounded. Cingulum laevigate, 6–12 μ wide; dark thickened inner ridge 1–3 μ wide and an outer, thinner zone of greater width. Distal surface has characteristic sculpture of small, irregularly arranged muri 2–3 μ wide, seldom connecting, infrequently small lobes project at cingulum's periphery.

Dimensions. (20 specimens.) Over-all diameter 33–55 μ . Body diameter 18–30 μ .

Holotype. Slide O3V16–9 (A–1). Location 47 $\times$ 125 (Ref. 31 $\times$ 116.5).

Description. Holotype 44 $\times$ 48 μ over-all, body 30 $\times$ 30 μ . Cingulum laevigate, 8–10 μ wide, inner dark ridge 2 μ wide. Laesurae three-fourths of radius, lips 1 μ wide, trilete open. Distal muri 2 μ wide, irregularly arranged.

Discussion. The species generally resembles spores of the arborescent lycopods. However, the distal hemisphere consistently bears a few muri-like thickenings, some of which terminate in enlarged knobs at the cingulum's outer margin. The muri have no particular arrangement, seldom connect, and are few in number and difficult to discern. On the basis of Neves's (1961) characterization of *Knoxisporites* on the presence of an equatorial cingulum and distal muri, the spore is tentatively assigned to that genus.

Knoxisporites triradiatus Hoffmeister, Staplin, and Malloy 1955

Plate 60, figs. 6, 7

Description. Radial, trilete, circular outline. Prominent cingulum is regular on individual specimens, 6–11 μ in width. Distal muri 6–10 μ in width. Laesurae distinct, straight,

extending almost to cingulum; lip development of about $1\ \mu$ on either side of commissure in some specimens but is not a consistent feature. Proximal and distal surfaces smooth.

Dimensions. (25 specimens.) Over-all diameter 48–78 μ .

Discussion. There appears to be some variation in the species, but most of this is only superficial and due largely to difference in specimen size and degree of distortion in preservation.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; Kentucky 'A' Seam coal, Kanawha formation, lower Pottsville, Harlan County, Kentucky.

Knoxisporites stephanephorus Love 1960

Plate 60, figs. 10–14

Description. Proximal ring 6–10 μ wide; distal equatorial ring 5–7 μ wide; distal polar boss 7–15 μ in diameter.

Dimensions. (50 specimens.) Over-all diameter 30–60 μ .

Discussion. Love (1960) differentiated this species from *K. rotatus* primarily on the basis of the thickening at the distal pole. In addition he considered the interradian thickening joining the rings to be more strongly developed in *K. rotatus*, while the lip structures in *K. stephanephorus* were more prominent than in *K. rotatus*. He noted some variation in the equatorial thickenings in his specimens. However, such a transition of developmental characters is present in the Springer specimens as to suggest the impossibility of distinguishing between these two species. Plate 60, fig. 11 presents a distinct distal platelet or boss, but it lacks interradian connexions between the equatorial rings. Plate 60, fig. 12 has well-defined interradian connexions but the outer or proximal ring is indistinct. Similarly the thickened lip structures lack consistency, although Love (1960) cited them as being present and narrowing to a point proximally. In Plate 60, figs. 12, 13 these are present the length of the rays, in Plate 60, fig. 14 they accompany the rays no more than one-third their length, and in Plate 60, fig. 10 they are completely lacking. In this study, specimens have been noted with all the characteristics of *K. stephanephorus* except for the distal boss (Pl. 60, fig. 10); others with boss present have no other features of the species. The species, *sensu* Love, is represented in the Springer. However, it is evident that these are developmental transitions which include more than one species, but as the genus is presently being studied by a working group of C.I.M.P. a redefinition is not undertaken here.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus NEXUOSISPORITES gen. nov.

Type species. *N. comtus* sp. nov.

Diagnosis. Radial, trilete, subcircular to subtriangular, margin slightly undulating. Laesurae simple, extending one-half to two-thirds radius. Spore body covered distally

by tightly packed convolutions. An unornamented cingulum is attached to the spore, although it often appears zonate because of the convolutions pushed on to it. An irregular, thickened ring rests on the distal surface. Its width varies considerably on a single specimen. Though not always completely developed, portions of the ring are always present.

Nexuosisporites comtus sp. nov.

Plate 65, figs. 6–8

Diagnosis. Radial, trilete, subcircular to subtriangular, margin slightly undulating. Laesurae simple, 9–18 μ long, extending one-half to two-thirds radius. Spore body covered distally by tightly packed convolutions, 3 μ high, 2–3 μ wide, with less than 1 μ between; some minor ornamentation occasionally developed proximally. An unornamented cingulum 5–12 μ thick (width remains constant on individual specimens) is attached to spore. Frequently there is a row of pits at the line of attachment, and the cingulum occasionally appears zonate because of the convolutions pushed on to it. A thickened ring rests on the distal surface. Though probably centred originally, it is often pushed to one side as an effect of compression. This ring is very irregular and its width varies considerably on individual specimens, ranging from 3 to 10 μ , 6 to 16 μ , to 6 to 12 μ . It sometimes appears to consist of connected globules. Ring diameters range from 24 μ to 34 μ , centre diameters from 3 μ to 10 μ . Though not always completely developed, recognizable portions of the ring are always present.

Dimensions. (25 specimens.) Over-all diameter 42–60 μ .

Holotype. Slide O3V16–11 (6). Location 48.5 $\times$ 125.5 (Ref. 31.7 $\times$ 116.9).

Description. Holotype 48 $\times$ 54 μ . Radial, trilete, subcircular, margin slightly undulating. Convolutions quite distinct and well defined, 2 μ wide, 3 μ high, 1 μ apart. Cingulum 12 μ wide, smooth. Trilete 12–16 μ long, extends to body margin. Distal ring well-formed, outline irregular, 10 μ across centre, 30 μ diameter, and ranging from 6 μ to 11 μ in width. Spore wall thin.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus STENOZONOTRILETES (Naumova) Hacquebard 1957

Type species. *S. conformis* Naumova 1953.

Stenozonotriletes cf. *spetcandus* Naumova 1953

Plate 61, fig. 1

Description. Radial, trilete, roundly subtriangular. Laesurae distinct, straight, extending nearly to body margin, commissure distinct; lips smooth, elevated, 4–6 μ wide. Wall distinct, 7–10 μ wide. Body laevigate.

Dimensions. (15 specimens.) Over-all diameter 55–78 μ .

Discussion. There is no definite assurance that this is the spore described by Naumova

(1953), and the assignment is based upon a comparison with the probable assignment by Playford (1962).

Genus CRASSISPORA Bhardwaj 1957

Type species. Crassispora (Planisporites) ovalis Bhardwaj 1957.

Crassispora (Planisporites) kosankei (Potonié and Kremp) Bhardwaj 1957

Plate 61, fig. 10

1955 *Planisporites kosankei* Potonié and Kremp, p. 71, pl. 13, figs. 208–13.

1957 *Apiculatisporis apiculatus* Dybová and Jachowicz, pp. 87–89, pl. 15, figs. 1–4.

1964 *Crassispora kosankei* (Potonié and Kremp) Bhardwaj; Sullivan, p. 376, pl. 60, figs. 13–15.

Description. Spores spheroidal to elliptical, trilete. Rays simple and difficult to discern, extending two-thirds distance of spore radius, rarely intact, usually split open to form characteristic triangular opening; triangular aperture ranging from $30 \times 30 \mu$ to $40 \times 45 \mu$, size of opening appearing to have no relationship to size of spore. Exine covered with closely spaced coni situated $1.5\text{--}4.5 \mu$ apart, $2\text{--}3 \mu$ wide at their bases, and averaging 1.5μ in length. Spores variously plicate, usually with thickened equatorial zone (*crassitudo* of Bhardwaj) $7\text{--}10 \mu$ wide about entire spore margin. Wall distinct, $3\text{--}6.5 \mu$ thick.

Dimensions. (25 specimens.) Diameter $56\text{--}72 \mu$, characteristic coni are variable in size; some specimens do not have them exceeding 1μ in length, while on others they measure up to 2μ . The majority of coni are about 1.5μ in length.

Discussion. Dybová and Jachowicz (1957) established three forms in the species. The Springer spores compare most closely with their form *media*, but there is a sufficient gradient in over-all size and coni characters in the Springer specimens to prevent definite assignment to any of the forms. They did not note the rather striking triangular gap resulting from the rupture of the trilete suture. It is of such usual occurrence that it seems to be a useful diagnostic feature; it is evident in all of their illustrations. Bhardwaj (1957) described the triangular slit and considered it to be a diagnostic feature.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; Livingston and New Livingston Coals, Gizzard formation, lower Pennsylvanian, Rockcastle County, Kentucky; Lily Coal, Breathitt formation, lower Pennsylvanian, Laurel County, Kentucky.

Genus CRISTATISPORITES (Potonié and Kremp) Butterworth, Jansonius, Smith, and Staplin 1964

Type species. C. indiguabundus (Loose) Potonié and Kremp 1954.

Cristatisporites indignabundus (Loose) Butterworth *et al.* 1964

Plate 61, fig. 2

1932 *Sporonites indignabundus* Loose in Potonié, Ibrahim, and Loose, p. 451, pl. 19, fig. 51.

1954 *Cristatisporites indignabundus* (Loose) Potonié and Kremp, p. 142, pl. 20, fig. 100 (8).

1964 *Cristatisporites indignabundus* (Loose) Potonié and Kremp; Staplin and Jansonius, p. 108, pl. 19, figs. 7, 9, 12, 14, 20; text-fig. 2c.

Description. Radial, trilete, roundly subtriangular. Proximal area finely granulose. Distal surface with prominent protuberances (warts of Staplin), frequently united at bases, up to $8.5\ \mu$ in length and $5\ \mu$ wide; protuberances usually with setose apices; smaller and more widely separated towards outer margin. Zona not clearly defined. Laesurae usually pronounced, slightly raised, lips $1.5\ \mu$ wide; rays reaching to body margin, occasionally appear to extend on zona.

Dimensions. (25 specimens.) Equatorial diameter $45\text{--}60\ \mu$. Diameter of body approximately $20\text{--}23\ \mu$.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Genus CINCTURASPORITES (Hacquebard and Barss) Bhardwaj and Venkatachala 1962

Type species. *C. altilis* Hacquebard and Barss 1957.

Cincturasporites minimus sp. nov.

Plate 61, fig. 3

Diagnosis. Spore spherical, trilete, cingulum present $6\text{--}9\ \mu$ wide, but not pronounced. Distal muri forming loose reticulum, muri $7\text{--}11\ \mu$ wide.

Dimensions. (5 specimens.) Over-all diameter $65\text{--}86\ \mu$.

Holotype. Slide O3V16-10 (B-1). Location 50×111 (Ref. 32.5×117.9).

Description. Holotype $84\times 86\ \mu$. Cingulum indistinct but attains measurable width of $9\ \mu$. Distal surface with muri $7\text{--}8.5\ \mu$ in width, radiating to form loose reticulum with

EXPLANATION OF PLATE 61

All figures $\times 500$ unless otherwise indicated.

Fig. 1. *Stenozonotriletes* cf. *spetcandus* Naumova 1953. Proximal surface; Slide O3V17-7 (1), location 45.2×112 (Ref. 31.3×117.7).

Fig. 2. *Cristatisporites indignabundus* (Loose) Butterworth *et al.* 1964. Distal surface; Slide O3V16-9 (B-2), location 41.8×107.6 (Ref. 31.7×118.2).

Fig. 3. *Cincturasporites minimus* sp. nov. Holotype. Slide O3V16-10 (B-1), location 50×111 (Ref. 32.5×117.9).

Fig. 4. *Cincturasporites magnus* sp. nov. Holotype. Proximal surface; Slide O3V16-14 (6), location 17×119 (Ref. 33×117).

Fig. 5. *Trochospora mastospinosa* sp. nov. Holotype. Proximal surface; Slide O3V16-9 (A-1), location 12.4×124.3 (Ref. 31×116.5).

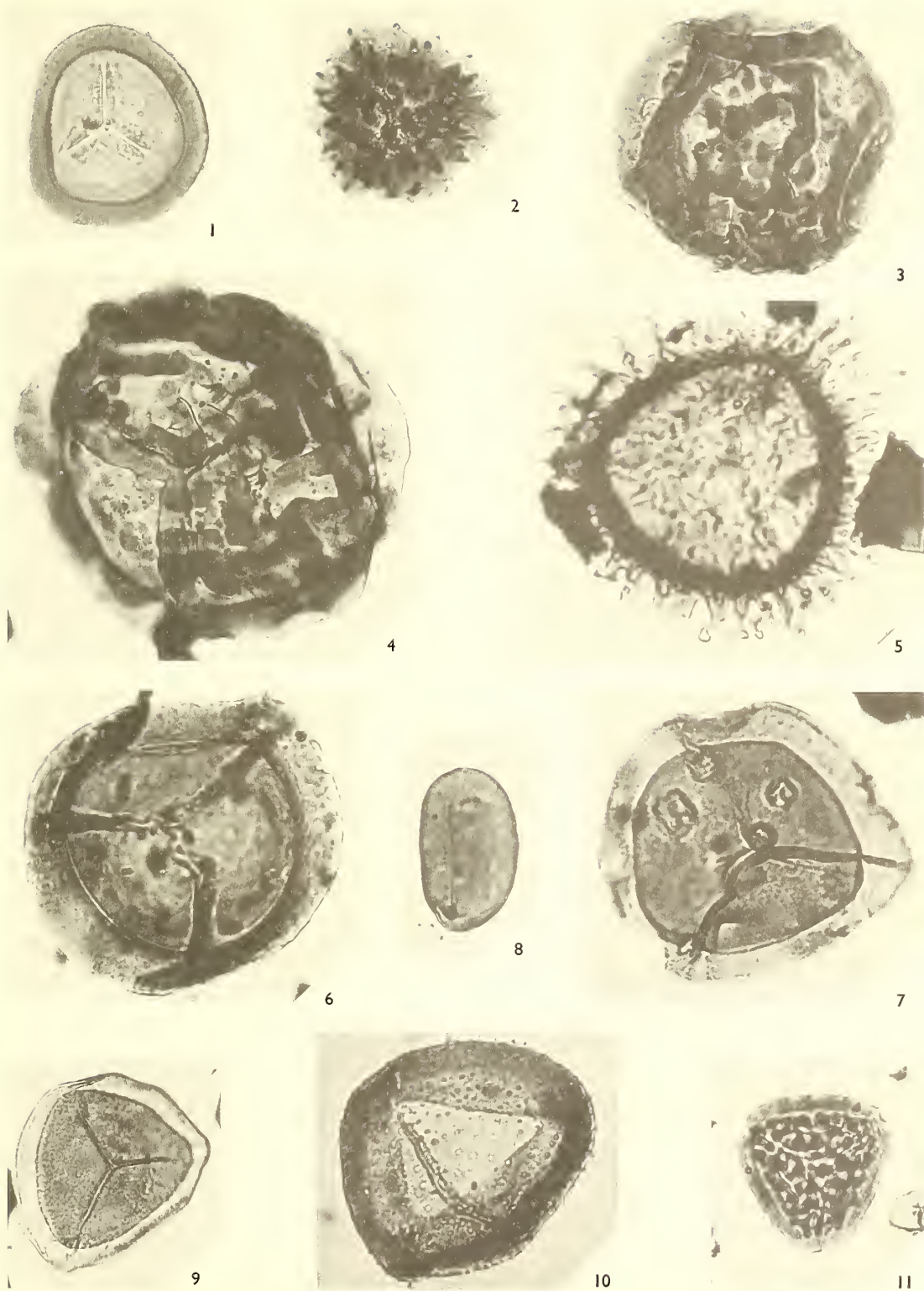
Figs. 6, 7. *Cirratriradites rusticus* sp. nov. 6, Proximal surface; Slide O3V16-4 (1), location 8×125.5 (Ref. 30.3×117.7). 7, Holotype. Proximal surface; Slide O3V16-9 (6), location 21.2×118 (Ref. 33.9×119.1).

Fig. 8. *Laevigatisporites ovalis* Kosanke 1950. Proximal surface; Slide O3V16-11 (6), location 33.5×124 (Ref. 31.7×116.9).

Fig. 9. *Cirratriradites leptomarginatus* sp. nov. Holotype. Proximal surface; Slide O3V17-1 (3), location 11.6×107.6 (Ref. 31×119.5).

Fig. 10. *Crassispora* (*Planisporites*) *kosankei* (Potonić and Kremp) Bhardwaj 1957. Proximal surface; Slide O3V16-13 (1), location 18.6×114 (Ref. 39.7×118.2).

Fig. 11. *Savitrissporites nux* (Butterworth and Williams) Sullivan 1964. Distal surface; Slide O3V16-11 (6), location 18.2×108 (Ref. 31.7×116.9).



lacunae up to $10 \times 23 \mu$. Oval, knob-like protuberances $4-7 \mu$ in diameter are a prominent distal wall feature. No discernible ornamentation on wall. Laesurae indistinct, limited to central body.

Discussion. The species is distinguished by elaborate thickenings on the distal side which extend on to the cingulum, obscuring it and rendering accurate measurements difficult. The rays are thin, and the heavy muri obscure them. Usually three or four loosely knit lacunae are formed, but no consistent ornamentation pattern is evident.

Comparison. Among described species only *C. radialis* Bhardwaj and Venkatachala 1962 possesses as elaborate distal ornamentation. However, their species differs greatly in its larger size, well-defined cingulum and laesurae, and in the presence of characteristic radiating thickenings in the cingulum. A slight resemblance to *Convolutispora* may be suggested by the irregular thickenings, but the resemblance is only superficial and the presence of a cingulum in *C. minimus* suffices to distinguish it from the convolute spores.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Cincturasporites magnus sp. nov.

Plate 61, fig. 4

Diagnosis. Spherical, trilete with prominent labial ornamentation. Cingulum distinct $8-17 \mu$ wide. Distal muri irregularly distributed, up to 12μ wide.

Dimensions. (10 specimens.) Over-all diameter $90-125 \mu$.

Holotype. Slide O3V16-14 (6). Location 17×119 (Ref. 33×117).

Description. Holotype $112 \times 121 \mu$. Cingulum distinct, laevigate, undulating to give a variable width of $8-12 \mu$. Distal surface with muri $6-12 \mu$ wide, forming irregular convolutions but not reticulate. Rounded protuberances averaging 10μ in diameter scattered about distal surface. No discernible wall ornamentation. Laesurae distinct, 35μ long, extending three-fourths distance to body margin, and with ray muri $7.5-10 \mu$ wide.

Comparisou. The larger size, well-defined cingulum, and laesurae, distinguish this species from *C. minimus*. The muri do not form a loose reticulum, although there is occasional slight branching. The muri lie in loose convolutions, and in the holotype one nearly encircles the entire distal periphery. The lip and cingulum features compare with *C. literatus* (Waltz) Hacquebard and Barss, but *C. magnus* is considerably larger, has a greater degree of muri ornamentation, and does not possess the row of punctations characteristic of the lips of *C. literatus*.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Discussion. Some disagreement already exists as to the proper limits of this genus, and the original designation by Hacquebard and Barss (1957) is certainly too wide. Moreover, Bhardwaj and Venkatachala (1962) pointed out in their emendation that the diplotype possessed distal ornamentation not included in the original description. The

specimens described here are considered to fall within the limits of the Bhardwaj and Venkatachala emendation or of Hacquebard and Barss (*sensu C. literatus*). We reject such species as *C. sulcatus*, *C. altilis*, *C. irregularis*, and *C. stenozonalis*. It is also our opinion that the broad labra are not sufficient reason for transfer to *Labiadensites* as suggested by Bhardwaj and Venkatachala (1962). It also seems quite certain that Winslow's (1962) *Reticulatisporites crassus* should be included within *Cincturaspores*.

Genus TROCHOSPORA gen. nov.

Type species. T. mastospinosa sp. nov.

Diagnosis. Spores radial, trilete; convexly subtriangular. Laesurae distinct, lips prominent, sinuous, extending to body margin. Narrow, thickened cingulum present. Distal surface conspicuously sculptured with large mammoid spinose processes, which are more numerous in the equatorial region than in the distal polar area.

Trochospora mastospinosa sp. nov.

Plate 61, fig. 5; text-fig. 4

Diagnosis. Spores radial, trilete, convexly subtriangular. Spore body wall distinct, 2–3 μ thick, laevigate. Laesurae sinuous, lips prominent, 35–40 μ long, length equal to body radius. Cingulum narrow, 4–6 μ wide. Prominent spines restricted to distal side, proximal surface unornamented. Spines 15–30 μ in length, enlarged basal portion up to 8.5 μ in width, apices setose to mammoid.

Dimensions. (5 specimens.) Over-all diameter 90–125 μ . Body diameter 65–80 μ .

Holotype. Slide O3V16–9 (A–1). Location 12.4 $\times$ 124.3 (Ref. 31 $\times$ 116.5).

Description. Holotype 120 $\times$ 122 μ , subtriangular; laesurae 35–37 μ long, extending to body margin, sinuous and with prominent labial structure to 7 μ in height. Cingulum 5–6 μ wide with irregular margin. Prominent spines 15–30 μ long on distal surface and more closely spaced towards equatorial region; processes have enlarged, often bulbous bases, which are up to 8.5 μ in width. Apices of processes of various types, but generally mammoid; however, apices are sometimes falcate, setose, or bulbous (text-fig. 4).

Discussion. This genus bears considerable resemblance to the densospores, but the thickened darkened area encircling the body appears to be a relatively narrow cingulum and not a zona. An appearance of having a zona or wide rim is further produced by the extension of the processes. There is some similarity to *Cristatisporites* which is described as having mammoid or setose small granules or apiculae. It also resembles *Spinozonotriletes* Hacquebard in the spines and their distribution, but *Trochospora* lacks the enveloping exine layer (perispore?).

Genus SAVITRISPORITES Bhardwaj 1955

Type species. S. triangulus Bhardwaj 1955.

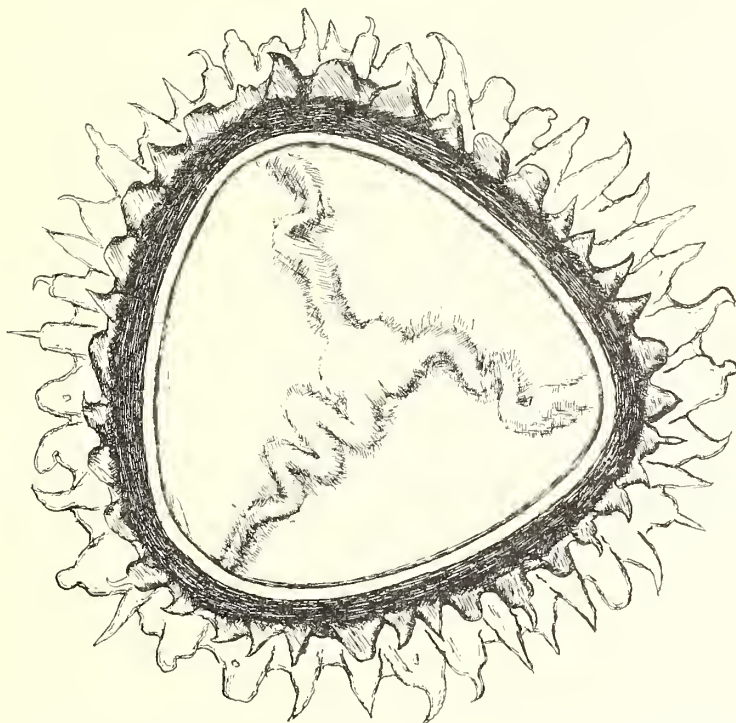
Savitrissporites nux (Butterworth and Williams) Sullivan 1964

Plate 61, fig. 11

1958 *Callisporites nux* Butterworth and Williams, p. 377, pl. 3, figs. 24, 25 and text-fig. 2.

1964 *Savitrisporites nux* (Butterworth and Williams) Sullivan, pp. 373–4, pl. 60, figs. 1–5.

Description. Radial, trilete, subtriangular in equatorial outline, interrarial margins straight to slightly convex. Solid cingulum 5–8 μ wide. Laesurae straight, simple, commissure usually visible; length 16–25 μ , extending to body margin. Ornamentation of broad, concentric distal ridges. Ridges are seldom continuous but are composed of short, closely spaced, irregularly crested components. Continuous ridges do often border the



TEXT-FIG. 4. *Trochospora mastospinosa* gen. and sp. nov. Proximal surface; Slide O3V16–9 (A-1), location 12.4 × 124.3 (Ref. 31 × 116.5).

laesurae, but components of the other ridges, although appearing continuous at low magnification seldom exceed 10 μ in length.

Dimensions. (25 specimens.) Equatorial diameter 40–60 μ .

Discussion. The rounded apices occasionally bear shallow notches in the cingulum. Usually only one apex on a specimen is indented, rarely two, and no specimens were observed with all three apices indented. Such a feature was not noted by Butterworth and Williams (1958), and it does not appear with sufficient regularity to warrant specific division. Sullivan (1964a) has established *Callisporites* as a junior synonym of *Savitrisporites*. Bhardwaj's (1955) genotype is from the Stephanian A; we have encountered spores from U.S. deposits of corresponding age which conform to Bhardwaj's description but differ markedly from *Callisporites* (*sensu* Butterworth and Williams). Geological time differences are no absolute criteria for differentiation, but the large time difference

between the Sullivan (1964a) and Bhardwaj (1955) assemblages, plus the apparent morphological differences, suggest that such an emendation is not acceptable. However, Sullivan (*personal communication*) has shown the writers evidence of morphological variations without demonstrable discontinuities in this taxon. In view of the fact that he has also personally examined type material, and Dr. M. A. Butterworth has collaborated on this examination and concurred with his findings, it is only reasonable to accept his emendation.

Other occurrences. Surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; subsurface Springer formation, Anadarko Basin.

Infraturma ZONATI Potonié and Kremp 1954
Genus CIRRATRIRADITES Wilson and Coe 1940

Type species. *C. maculatus* Wilson and Coe 1940.

Cirratriradites leptomarginatus sp. nov.

Plate 61, fig. 9

Diagnosis. Radial, trilete, convexly subtriangular. Laesurae distinct, straight with slight lip development, commissures visible at high magnification; rays usually extending two-thirds to four-fifths of central body radius, occasionally individual rays extend on the equatorial zona. Central body minutely punctate. Thin, membranous equatorial zona 7.5–10 μ in width, minutely granulose, bordered about its outer periphery by thickened rim about 1.5 μ thick.

Dimensions. (10 specimens.) Over-all equatorial diameter 56–66 μ . Body diameter 38–55 μ .

Holotype. Slide O3V17-1 (3). Location 11.6 $\times$ 107.6 (Ref. 31 $\times$ 119.5).

Description. Holotype 60 $\times$ 63.5 μ over-all. Thin, membranous zona 8 μ wide, including slightly thickened marginal rim 1.5 μ wide. Laesurae distinct, straight, 20 μ long, about four-fifths of body radius; no pronounced labial development. Spore body punctate; zona granulose.

Discussion. There is some reservation in assigning this spore to *Cirratriradites* since that genus is usually described as having strongly demarcated lips raised above the body and a broad equatorial zona. The zona here cannot be considered as broad.

Comparison. It resembles *Angulisporites* (Bhardwaj 1954), but *Angulisporites* described from Stephanian age deposits has a granulose body and some zonation of the zona.

Cirratriradites rusticus sp. nov.

Plate 61, figs. 6, 7

Diagnosis. Radial, trilete, convexly subtriangular. Laesurae distinct, sinuous, extending on to zona, frequently to the equator; bordered by conspicuous, strongly developed flexuous lips having a maximum height of 15 μ . Zona 12–25 μ in width, faintly granulose, intact specimens with peripheral border or rim about 3 μ wide; specimens frequently

corroded about outer periphery and zona presents irregular, somewhat fringed appearance. Spore body wall $1.5\text{--}3\ \mu$ thick, granulose.

Dimensions. (25 specimens.) Over-all diameter $60\text{--}115\ \mu$ (average $85\text{--}90\ \mu$). Body diameter $50\text{--}85\ \mu$ (average $60\text{--}65\ \mu$).

Holotype. Slide O3V16-9 (6). Location 21.2×118 (Ref. 33.9×119.1).

Description. Holotype $86 \times 96\ \mu$ over-all, body $60 \times 66\ \mu$. Zona $16\ \mu$ wide, minutely granulose, bordered by rim $3\ \mu$ wide. Laesurae distinct, sinuous, extending on to zona, attaining maximum length of $42\ \mu$. Body wall $1.5\ \mu$ thick, granulose.

Discussion. The species shows some similarity to *Leiozonotriletes* Hacquebard 1957, but the latter is clearly not zonate and has a mesosporoid enclosed by the exoexine.

Cirratriradites saturni (Ibrahim) Schopf, Wilson, and Bentall 1944

Plate 62, fig. 1

Dimensions. (25 specimens.) Over-all equatorial diameter $70\text{--}105\ \mu$. Body diameter $55\text{--}65\ \mu$. Flange $13\text{--}20\ \mu$ in width. Distal fovea $20\text{--}30\ \mu$ in diameter.

Discussion. *C. saturni* has long been regarded as the type species of the genus, but Wilson (1966) has recently restored *C. maculatus* to the status of type species.

Other occurrences. Very common in subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus REINSCHOSPORA Schopf, Wilson, and Bentall 1944

Type species. *R. speciosa* (Loose) Schopf, Wilson and Bentall syn. *R. bellitas*.

Reinschospora speciosa (Loose) Schopf, Wilson, and Bentall 1944

Plate 62, fig. 3

1934 *Alatisporites speciosus* Loose, p. 151, pl. 7, fig. 1.

1944 *Reinschospora bellitas* Bentall in Schopf, Wilson, and Bentall, p. 53, fig. 2.

1955 *Reinschospora speciosa* (Loose) Schopf, Wilson, and Bentall; Horst, p. 187, pl. 21, figs. 38-39.

1956 *Reinschospora speciosa* (Loose) Schopf, Wilson, and Bentall; Potonié and Kremp, p. 132, pl. 19, fig. 419.

Description. Radial, trilete; body subtriangular with concave sides. Laesurae distinct, straight, about $30\ \mu$ long, extending nearly to equatorial margin; commissure distinct, lips narrow, not exceeding $1\ \mu$ in width. Prominent fimbriate corona with fine, narrow fimbriae so closely spaced as to appear fused; fimbriae number $40\text{--}50$ between ray extremities, attain maximum length of $17\text{--}23\ \mu$ in central interradian area and minimum length of $5\text{--}7.5\ \mu$ at apices. Corona originates proximally about $5\ \mu$ beyond the spore wall. Spore body minutely punctate, wall $1.5\ \mu$ thick.

Dimensions. (15 specimens.) Over-all diameter $77\text{--}85\ \mu$. Body diameter $52\text{--}65\ \mu$.

Comparison. The Springer specimens differ only from Bentall's (Schopf, Wilson, and Bentall 1944) description of *R. bellitas* in being minutely punctate. However, the wall

feature is often difficult to discern unless at high magnification. The punctations are not nearly so pronounced as in *R. punctata* Kosanke 1950, and the fimbriate elements are much finer and longer in *R. speciosa*. Bentall recognized the similarity of his *R. bellitas* to *R. speciosa* Loose but considered the size difference too great to permit assignment to the latter. However, Horst (1955) noted an error in Loose's figure and extended the size from 54 μ to 81 μ .

Other occurrences. Bentall's material was from the Gizzard formation, lower Pennsylvanian, Marion County, Tennessee. The authors have observed the species from the Lily Coal, Breathitt formation, lower Pennsylvanian, Laurel County, Kentucky.

Infraturma MEMBRANATI Neves 1961

Genus PROPRISPORITES Neves 1958

Type species. *P. rugosus* Neves 1958.

Propriporites rugosus Neves 1958

Plate 62, fig. 4

Description. Spore minutely punctate. Laesurae straight, length two-thirds body radius, lips very thin. Perisporal folds projecting 6–8 μ .

Dimensions. (5 specimens.) Over-all diameter 80–85 μ . Body diameter 65–70 μ .

Discussion. *P. rugosus* is very rare in the Springer sediments, whereas *P. laevigatus* occurred in large numbers in several samples.

EXPLANATION OF PLATE 62

All figures $\times 500$ unless otherwise indicated.

Fig. 1. *Cirratiradites saturni* (Ibrahim) Schopf, Wilson, and Bentall 1944. Proximal surface; Slide O3V16–3 (6), location 20 $\times$ 125.2 (Ref. 33 $\times$ 117.9).

Fig. 2. *Endosporites micromanifestus* Hacquebard 1957. Proximal surface; Slide O3V17–1 (5), location 11.5 $\times$ 115.3 (Ref. 32 $\times$ 119).

Fig. 3. *Reinschospora speciosa* (Loose) Schopf, Wilson, and Bentall 1944. Proximal surface; Slide O3V16–6 (1), location 39.8 $\times$ 117 (Ref. 31.4 $\times$ 118).

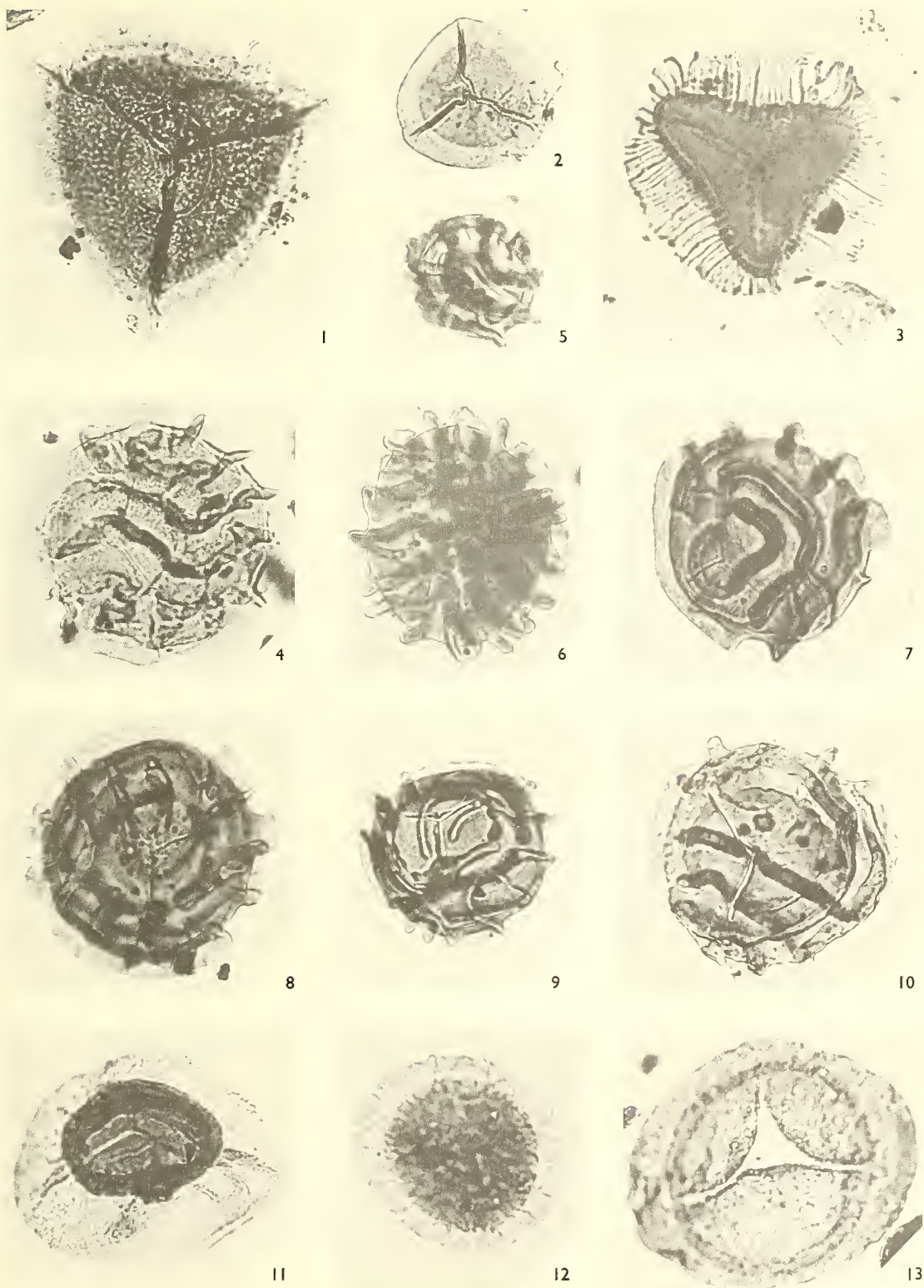
Fig. 4. *Propriporites rugosus* Neves 1958. Proximal surface; Slide O3V16–10 (1), location 53.5 $\times$ 112 (Ref. 30 $\times$ 117.6).

Figs. 5–10. *Propriporites laevigatus* Neves 1961. 5, Distal surface; Slide O3V16–3 (5), location 37 $\times$ 122.8 (Ref. 33.7 $\times$ 118). 6, Proximal surface; Slide O3V16–11 (1), location 50 $\times$ 119.5 (Ref. 32 $\times$ 118.7). 7, Proximal surface; Slide O3V16–9 (6), location 51 $\times$ 124.6 (Ref. 33.9 $\times$ 119.1). 8, Proximal surface; Slide O3V16–3 (6), location 22.5 $\times$ 107.4 (Ref. 33 $\times$ 117.9). 10, Proximal surface; Slide O3V16–10 (2), location 28 $\times$ 115.3 (Ref. 53 $\times$ 117.7).

Fig. 11. *Auroraspora solisortus* Hoffmeister, Staplin, and Malloy 1955. Slide O3V16–9 (B-2), location 36.6 $\times$ 118.5 (Ref. 31.7 $\times$ 118.2).

Fig. 12. *Hymenospora caperata* sp. nov. Holotype $\times 750$. Slide O3V16–9 (A-1), location 43.6 $\times$ 111.9 (Ref. 31 $\times$ 116.5).

Fig. 13. *Schulzospora rara* Kosanke 1950. Proximal surface; Slide O3V16–4 (R-1), location 18.1 $\times$ 121 (Ref. 32.3 $\times$ 118.7).



Proprisporites laevigatus Neves 1961

Plate 62, figs. 5–10

Description. Spores laevigate. Laesurae straight, length about three-quarters body radius, lips thin, not exceeding $1\ \mu$. The laevigate, perisporal membrane in the equatorial plane projects $6\text{--}7\ \mu$, and the folded membrane in polar view gives the appearance of ridges $3\text{--}5\ \mu$ in width.

Dimensions. (50 specimens.) Over-all diameter $45\text{--}90\ \mu$.

Discussion. The specimens in the Springer have a greater size variation than Neves (1961) cited. However, the average size range is $65\text{--}80\ \mu$, and about 75 per cent. of the spores studied fell within a $68\text{--}72\ \mu$ size group. Only a few rare specimens were in the $45\text{--}50\ \mu$ (Pl. 62, fig. 5) range and probably represent anomalies. There is also a variation in the number of long folds, as well as in size. Plate 62, fig. 10 illustrates the minimum number observed with only four lobes appearing to encircle the body, while Plate 62, fig. 6 shows the maximum attained with seventeen lobes or folds present. The latter is an extreme instance, and Plate 62, figs. 7, 8 represent the usual character. However, the gradation both in size and fold characteristics precludes any clearcut specific distinction based on these features. A character not mentioned by Neves but appearing in his illustrations is the occurrence of isolated rounded bosses and small granular protuberances on the otherwise laevigate body. Plate 62, fig. 8 represents the maximum degree of occurrence of the granules, which are rounded, $1\text{--}5\ \mu$ in diameter, and usually in a small group on the distal mid-polar area. However they are not a consistent feature.

Jansonius (1962) proposed an emendation of *Proprisporites*, but the evidence he submits does not justify the change, and we reject it. In addition, it seems to tax credulity to extend this stratigraphically important Mississippian genus into the Triassic. Jansonius's comparison of *P. rugosus* with *Perotriletes perinatus* Hughes and Playford 1961 is similarly rejected on grounds of insufficient evidence.

Other occurrences. Both species are present in the subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma. An undescribed species of the genus has been recorded by the authors from the Stearns #1 coal, Gizzard formation, lower Pottsville, McCreary County, Kentucky. The spore cited as *Reticulatisporites* sp. 2 by Venkatachala and Beju (1962, pl. 1, figs. 22–24) is certainly *Proprisporites* and is probably *P. rugosus*.

Genus HYMENOSPORA Neves 1961

Type species. *H. palliolata* Neves 1961.

Hymenospora caperata sp. nov.

Plate 62, fig. 12

Diagnosis. Radial, trilete, circular outline. Laesurae indistinct, extending to, or nearly to, the body margin. Spore body covered by thin outer membrane, which forms a zonate-like margin about the body $4.5\text{--}7.5\ \mu$ in width; membrane wrinkled and distorted to give crinkled appearance. Spore body minutely punctate.

Dimensions. (20 specimens.) Diameter 35–52 μ .

Holotype. Slide O3V16–9 (A–1). Location 43·6 $\times$ 111·9 (Ref. 31 $\times$ 116·5).

Description. Holotype 43 $\times$ 44 μ . Membranous outer layer laevigate, extending 5–7·5 μ beyond body to produce zonate appearance; outer membrane densely plicated and appears wrinkled. Spore body minutely punctate. Laesurae extending nearly to spore margin, difficult to determine due to enveloping, wrinkled outer membrane.

Comparison. *H. palliolata* Neves, the only other described species, is considerably larger, possesses a laevigate body, and does not seem to have the degree of plication of the outer membrane. The rays of *H. caperata* are difficult to resolve, owing to the thickness of the outer membrane and its many plications. Although never conspicuous quantitatively, this spore is one of the most ubiquitous and has been noted in numerous other localities.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma; Kentucky 'C' seam coal, Kanawha formation, lower Pottsville, Harlan County, Kentucky.

Turma MONOLETES Ibrahim 1933
Subturma AZONOMONOLETES Luber 1935
Genus LAEVIGATOSPORITES Ibrahim 1933

Type species. *L. vulgaris* Ibrahim 1933.

Laevigatosporites ovalis Kosanke 1950

Plate 61, fig. 8

Description. Spores are bilateral, monolete, bean-shaped in longitudinal plan, oval in equatorial plan. Spore coat is laevigate, very thin (1 μ) with frequent minor folding. The monolete suture is distinct, simple, and one-half to three-fourths the length of the spore (22–36 μ).

Dimensions. (15 specimens.) Over-all length 42–60 μ . Width 26–38 μ .

Discussion. The spores have been placed in this species although there are some slight differences from Kosanke's description (1950). The Springer material does not seem to be as thick walled, and the question of lips is debatable. At very high power some of the specimens have tiny thickenings along the suture. Though not labial structures in the classic sense, these may be the lips referred to in the original description.

Genus MONOLETES (Ibrahim) Schopf, Wilson, and Bentall 1944

Type species. *M. ovatus* Schopf 1936.

Remarks. *Monoletes* is another example of the conflicting taxonomy so prevalent in plant microfossil research. The name was first used by Ibrahim (1933) for a spore group in an artificial system, but it was not used in a generic sense and no nomenclatural type was designated. Schopf (1936, 1938) used it in a generic sense, and Schopf, Wilson, and

Bentall (1944) published an emendation and designated *Monoletes ovatus* Schopf as the type species. However, recent workers tend to regard *Monoletes* as a division somewhat coordinate to the Reinsch (1884) genus *Triletes*. Potonié and Kremp (1954, 1956a) are foremost in using this treatment, and in their 1954 treatment they included *Monoletes* in the new genus *Schopfipollenites*, with *S. ellipsoides* as the type species. This classification does not clarify the taxonomy. *Monoletes* was originally meant to include typical bilateral spores, and Schopf, Wilson, and Bentall (1944) emended it to include the spores of a pteridospermic plant alliance such as the Whittleseyinae. Since this could include more than one genus, the genus will undoubtedly require refinement. However, *Schopfipollenites* does not resolve this problem since Potonié and Kremp created it for the Whittleseyinae spores also, thus still leaving *Monoletes* to include the majority of the bilateral spores. In our opinion *Monoletes* most nearly meets the natural designation of our spore.

Monoletes ovatus Schopf 1936

Plate 63, figs. 1, 2

Description. Bilateral, subovate; monolete suture medially deflected, ray about two-thirds length of spore body, measuring $105\text{--}40\ \mu$ in length; lips $4\text{--}5\ \mu$ wide on each side of commissure. Distal surface usually bearing two longitudinal grooves on expanded specimens; compressed specimens frequently with longitudinal folds parallel to groove. Body wall $5\text{--}10\ \mu$ thick. Thin, granular outer coat sometimes present, adhering closely to spore body; body proper laevigate.

Dimensions. (25 specimens.) Over-all dimensions $140\times 165\ \mu$ to $150\times 195\ \mu$. Body $135\times 160\ \mu$ to $145\times 180\ \mu$.

Discussion. In some specimens the distal grooves are absent, even in the case of excellent preservation. The grooves probably do not warrant the attention they have formerly received. Although Schopf (1938) distinguished *M. ellipsoides* from *M. ovatus* on the lack of such grooves, Winslow (1959) has noted that presence or absence of these features may be of limited diagnostic value. The Springer specimens are smaller than the size values given by Schopf (1938) for the species, but they are within the size of Winslow's material, several of which are referable to *M. ovatus*. Other than size, there are no features on which to differentiate these spores from those of Schopf.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Monoletes sp.

Plate 63, figs. 3, 4

Description. Bilateral, subovate; monolete suture medially deflected, ray often difficult to discern but measures up to $85\ \mu$ in length and over one-half length of body, lips $2\text{--}3\ \mu$ in width. Distal surface not bearing longitudinal grooves. Central body covered by a granulose membrane; spore body proper laevigate.

Dimensions. (25 specimens.) Over-all dimensions $90\times 120\ \mu$ to $120\times 140\ \mu$. Body $65\times 85\ \mu$ to $75\times 115\ \mu$.

Discussion. This particular *Monoletes* was numerous in only two samples (O3V16-9 and O3V17-2), and the manner in which a smaller body is enclosed within a surrounding membrane is very similar to *M. aureolus* Schopf. It lies considerably outside Schopf's (1938) minimum size of 200 μ , and does not display the bifurcating medial suture described for *M. aureolus*. Winslow (1959) encountered similar examples and suggested they might be 'sports' referable to *M. ovatus*, if fully developed. This seems a reasonable explanation for the Springer specimens, which have little to distinguish them from *M. ovatus* other than their small dimensions and loosely encompassing membrane.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Anteturma POLLENITES R. Potonié 1931
Turma SACCITES Erdtman 1947
Subturma MONOSACCITES Chitaley 1951
Genus ENDOSPORITES Wilson and Coe 1940

Type species. *E. ornatus* Wilson and Coe 1940.

Endosporites micromanifestus Hacquebard 1957

Plate 62, fig. 2

- 1956 *Hymenozonotrilites* aff. *variabilis* Naumova; Ischenko, p. 62, pl. 11, figs. 129-30.
- 1957 *Endosporites micromanifestus* Hacquebard, p. 317, pl. 3, fig. 16.
- 1960 *Auroraspora micromanifestus* (Hacquebard) Richardson, p. 51.
- 1963 *Endosporites micromanifestus* Hacquebard; Playford, p. 652, pl. 93, figs. 17-18.
- 1964 *Endosporites micromanifestus* Hacquebard; Playford, p. 37, pl. 11, fig. 2.

Dimensions. (50 specimens.) Over-all diameter 42-60 μ . Diameter of central body 30-48 μ .

Discussion. The specimens closely conform with previous descriptions of Hacquebard (1957) and Playford (1963, 1964). The spore is quite common in the Springer, particularly in sample O3V16-9.

Genus SCHULZOSPORA Kosanke 1950

Type species. *S. rara* Kosanke 1950.

Schulzospora rara Kosanke 1950

Plate 62, fig. 13

Description. Radial, trilete, spherical body. Bladder fold of 5-8 μ in width at body periphery. Bladder and body ornamentation finely punctate. Laesurae 23-28 μ in length, extending nearly to body margin, frequently split open, with minor lip development.

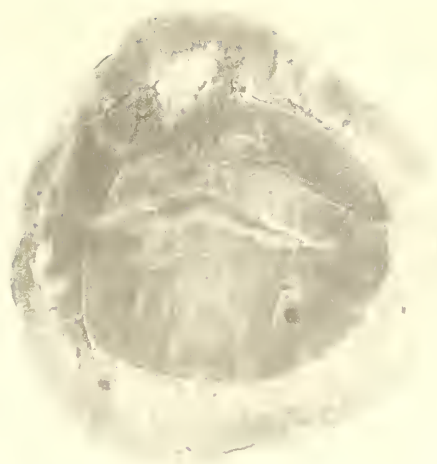
EXPLANATION OF PLATE 63

All figures $\times 500$ unless otherwise indicated.

- Figs. 1, 2. *Monoletes ovatus* Schopf 1936. 1, Distal surface; Slide O3V16-14 (6), location 55 $\times$ 122 (Ref. 33 $\times$ 117). 2, Proximal surface; Slide O3V17-1 (4), location 48.6 $\times$ 114.8 (Ref. 32 $\times$ 119.6).
- Figs. 3, 4. *Monoletes* sp. 3, Proximal surface; Slide O3V16-5 (3), location 22 $\times$ 126.8 (Ref. 33.7 $\times$ 118.2).
- 4, Partially torn perispore; Slide O3V16-10 (2), location 33 $\times$ 119 (Ref. 53 $\times$ 117.7).
- Fig. 5. *Cystoptychus velatus* sp. nov. Holotype. Proximal surface; Slide O3V16-9 (5), location 30.2 $\times$ 115 (Ref. 32.4 $\times$ 118.6).



1



3



5



2



4

Dimensions. (25 specimens.) Over-all diameter 66–92 μ . Body diameter 52–65 μ .

Discussion. The assignment to *S. rara* is based on the finely punctate ornamentation, the conspicuous folding of the bladder on the body, and the laesurae with spore coat frequently ruptured along the sutures. Although the dimensions of the Springer specimens are smaller than those cited by Kosanke (1950), they compare with those given for *S. cf. rara* Hoffmeister, Staplin, and Malloy (1955*b*). As Love (1960) has suggested, the specimen figured by Butterworth and Williams (1958) as *S. ocellata* is probably *S. rara*. On the basis of Horst's (1955) description of *S. ocellata*, any differentiation from *S. rara* is very difficult. An obliquity of the central body in the former seems to be the only means of distinguishing between the two species, and it is quite likely that examination of the types will result in their being analogous.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus FLORINITES Schopf, Wilson, and Bental 1944

Type species. *F. antiquus* Schopf, Wilson, and Bental 1944.

Florinites guttatus sp. nov.

Plate 64, figs. 1–3

Diagnosis. Bilateral, grains broadly elliptical, body spherical. Monolete suture 25–30 μ long, generally straight, frequently a distinct medial deflection of the suture is evident; occasionally the suture further develops a short, third ray, somewhat indistinct; rarely the vestigial ray develops to full length and forms a distinct trilete. Two prominent folds on the distal side of the body are oriented at right angles to the long axis of the spore, forming a narrow sulcus; although the folds have a considerable degree of uniformity (Pl. 64, fig. 1), they are often displaced inwardly or outwardly (Pl. 64, figs. 2, 3). The body is not enclosed by the bladder proper either distally or proximally, which is contrary to the classic generic description of the body being entirely enclosed by the bladder except for part of the distal side. The bladder proper is internally reticulate and does slightly overlap the body at the point of attachment. However, the dark tapering folds are features of the body and not of the bladder overlap. The spore body is enclosed within a delicate membrane, which is minutely granulose on the proximal side. However, on the distal side this membrane possesses a delicate, yet conspicuous, rugulate type of ornamentation consisting of an irregular, reticuloid pattern with segments 5–10 μ in diameter. Spore body proper is laevigate.

Dimensions. (50 specimens.) Over-all diameter 95–140 $\times$ 120–70 μ . Body diameter 45–85 $\times$ 65–95 μ .

Holotype. Slide O3V16–13 (A–2). Location 17.1 $\times$ 117.6 (Ref. 32.2 $\times$ 117.9).

Description. Holotype 103 $\times$ 145 μ over-all diameter, body 65 $\times$ 80 μ . Monolete suture 30 μ long. Two distinctive vertical folds on distal side of body; spore body covered by thin granulose membrane proximally and a coarser reticuloid membrane distally.

Discussion. The taxonomy of *Florinites* is not at all clear, and at present it includes a variety of monosaccate spores such as those with a well-developed trilete (*F. triletes*)

and others with a sulcus (*F. diversiformis*). The writers feel that there is little doubt but that this spore belongs in *Florinites*, yet the present description creates several problems. The bladder never encloses the body, whereas considerable importance has been attributed to this character in saccate generic designations. The germinal aperture with its variation is noteworthy, since Bhardwaj (1955) has regarded the presence or absence of a germinal opening as very important in distinguishing between genera (i.e. *Kosankeisporites* and *Illinites*). *Potoniisporites* is a monosaccate, monolete spore, but *F. guttatus* shows a gradation from monolete to trilete.

Comparison. *F. guttatus* perhaps compares most closely with *F. diversiformis* Kosanke in the general appearance presented by the body folds. However, Kosanke (1950) did not note the readily discernible and variable germinal suture. He did not note, or figure, the rugulate perispore-like covering of the distal body and the contrasting granulose proximal covering. An examination of several specimens of *F. diversiformis* from Kosanke's maceration No. 618 did not disclose these characteristics in his species. There are several saccate spores described with ornamentation similar to the distal pattern of *F. guttatus*. Peppers (1964, p. 43) figured a similar monosaccate grain which he described as polygonally areolate distally, but he did not formally describe the specimen, and properly speaking the ornamentation of *F. guttatus* probably cannot be regarded as areolae.

Other occurrences. Subsurface Springer formation, Anadarko Basin.

Florinites visendus (Ibrahim) Schopf, Wilson, and Bentall 1944

Plate 64, fig. 4

- 1933 *Reticulata-sporites visendus* Ibrahim, p. 39, pl. 8, fig. 66.
- 1944 *Florinites* (?) *visendus* (Ibrahim) Schopf, Wilson, and Bentall, p. 60.
- 1956 *Florinites visendus* (Ibrahim) Schopf, Wilson, and Bentall; Potonié and Kremp, p. 170, pl. 21, figs. 476-7.
- 1957 *Florinites visendus* (Ibrahim) Schopf, Wilson, and Bentall; Bhardwaj, p. 129, pl. 26, fig. 106.

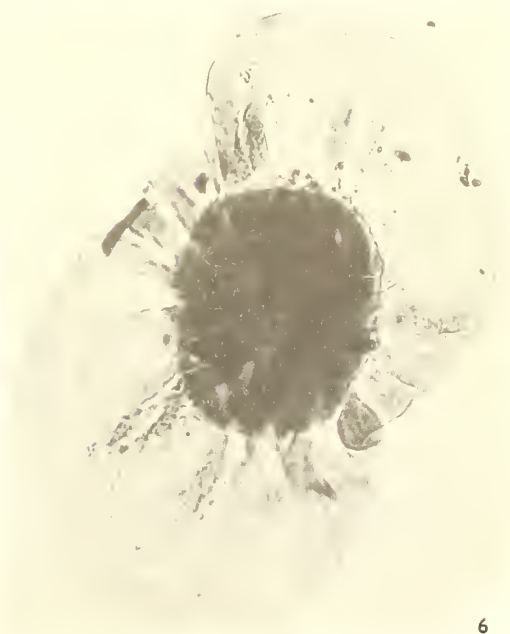
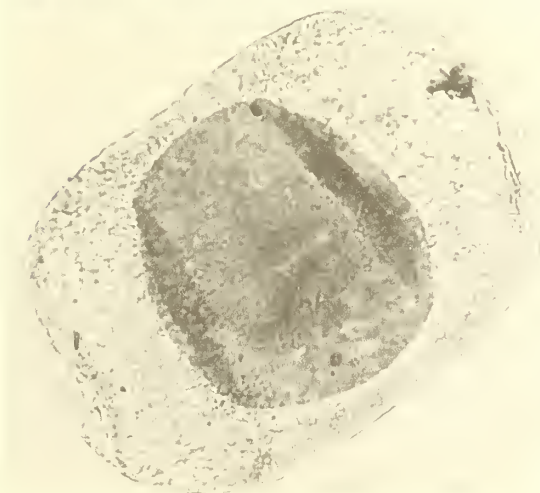
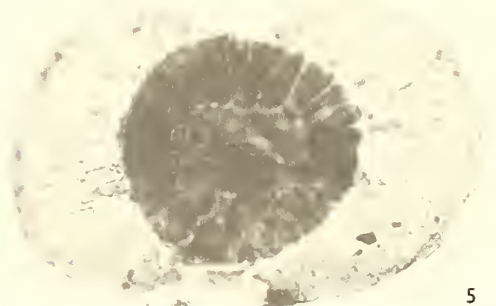
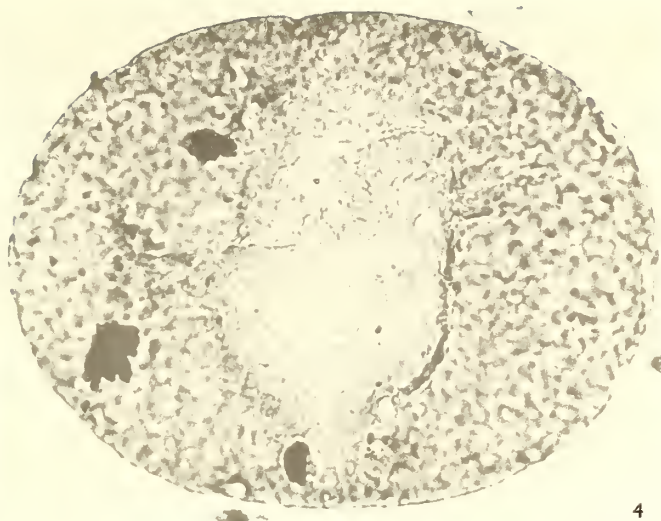
Description. Spore elliptical to circular in equatorial outline. Central body usually absent, indistinct in intact specimens. Bladder coarsely reticulate. No definite laesurae observed.

Dimensions. (50 specimens.) Equatorial diameter 130-240 μ .

EXPLANATION OF PLATE 64

All figures $\times 500$ unless otherwise indicated.

- Figs. 1-3. *Florinites guttatus* sp. nov. 1, Holotype. Proximal surface; Slide O3V16-13 (A-2), location 17.1 $\times$ 117.6 (Ref. 32.2 $\times$ 117.9). 2, Distal surface; Slide O3V16-11 (6), location 53 $\times$ 113 (Ref. 31.7 $\times$ 116.9). 3, Distal surface; Slide O3V16-11 (1), location 50.2 $\times$ 95.2 (Ref. 32 $\times$ 118.7).
- Fig. 4. *Florinites visendus* (Ibrahim) Schopf, Wilson, and Bentall 1944. Slide O3V16-3 (6), location 21.5 $\times$ 120.6 (Ref. 33 $\times$ 117.9).
- Figs. 5, 6. *Costatascychus crenatus* sp. nov. 5, Distal surface; Slide O3V16-3 (5), location 39 $\times$ 129 (Ref. 33.7 $\times$ 118). 6, Holotype. Distal surface; Slide O3V16-11 (5), location 42.5 $\times$ 108.6 (Ref. 32.6 $\times$ 117.8).



Discussion. The central body usually appeared to be missing, with the central spore region very thin and frequently displaying a slit-like opening. In a few instances damaged specimens were observed with a definite central body enclosed within the large bladder. The differential in size of reticulations between the central area and the saccus as described by Potonié and Kremp (1956a) was not observed in the Springer. Actually there appears to be little means of distinguishing *F. visendus* from *F. pumicosus* other than on size. This is generally an unreliable criterion when it is the sole difference, but in this instance there does appear to be a definite wide gap in the size ranges of the two species.

Other occurrences. Subsurface Springer formation, Anadarko Basin; subsurface Morrow formation, upper Pennsylvanian, Anadarko Basin; surface Wildhorse Mountain formation, Jackfork group, upper Mississippian, Le Flore County, Oklahoma.

Genus AURORASPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *A. solisortus* Hoffmeister, Staplin, and Malloy 1955.

Auroraspora solisortus Hoffmeister, Staplin, and Malloy 1955

Plate 62, fig. 11

Description. Radial, trilete. Central body laevigate, circular to subcircular. Laesurae distinct, slight lip development of $1-1.5\ \mu$, extending two-thirds to three-fourths central body radius. Thin, translucent bladder, frequently plicated, surface finely granulose; bladder width beyond central body, $15-20\ \mu$.

Dimensions. (25 specimens.) Over-all diameter $60-82\ \mu$ ($70-75\ \mu$ average). Diameter of central body $32-50\ \mu$ ($40-45\ \mu$ average).

Discussion. The body is rarely found covered with the thin membrane described by Hoffmeister, Staplin, and Malloy (1955b), but the specimens otherwise conform with the original diagnosis.

Other occurrences. Subsurface Springer formation, Anadarko Basin; surface Goddard formation, upper Mississippian, Johnston County, Oklahoma.

Genus COSTATASYCLUS gen. nov.

Type species. *C. crenatus* sp. nov.

Diagnosis. Spores bilateral, outline elliptical in transverse plane. Monosaccate, occasionally appearing bisaccate due to orientation. Central body outline circular to elliptical. Bladder intrareticulate; proximal side of body free, distal side characterized by radiating ribs about body periphery. Monolete, with occasional vestigial trilete.

Discussion. Specimens occasionally appear bisaccate due to compression distortion. There is some resemblance to *Rhizomaspora* (Wilson 1962), but the latter is definitely bisaccate. *Costatasyclus* is Wilson's (1965) Sporomorph D (pl. 3, fig. 8) reported from the Springer of the Ti Valley, Pittsburgh County, Oklahoma.

Costatascyclus crenatus sp. nov.

Plate 64, figs. 5, 6

Diagnosis. Monosaccate, bilateral and elliptical in transverse plane, body spherical. Bladder partially inserted on distal surface of body, proximal side free. The distal attachment of the bladder is characterized by a distinct series of folds about the body periphery, forming radiating ribs diverging toward the equator; the resulting structure is a row of deep crenulations around the periphery of the central body distally. The folds are twenty to thirty in number on a specimen, 20–25 μ in length and 5–7.5 μ in width. Suture indistinct, monolete, about one-fourth to one-third length of body, rarely with slight medial deflection, rarely forming a short vestigial ray at the point of deflection to give a trilete appearance. Bladder ornamentation intrareticulate. Spore body laevigate.

Dimensions. (50 specimens.) Over-all size 77 $\times$ 125 μ to 110 $\times$ 165 μ . Body dimensions 54 $\times$ 72 μ to 60 $\times$ 84 μ .

Holotype. Slide O3V16–11 (5). Location 42.5 $\times$ 108.6 (Ref. 32.6 $\times$ 117.8).

Description. Holotype elliptical in outline, central body spherical. Over-all size 99 $\times$ 165 μ ; body 54 $\times$ 67 μ . Radiating folds of bladder on distal side extend to 20 μ in length and are 5–7 μ in width.

Genus POTONIEISPORITES Bhardwaj 1954

Type species. *P. novicus* Bhardwaj 1954.

Potonieisporites elegans (Wilson and Kosanke) Wilson and Venkatachala 1964

Plate 66, fig. 1

1944 *Florinites elegans* Wilson and Kosanke, p. 330, fig. 3.

1964 *Potonieisporites elegans* (Wilson and Kosanke) Wilson and Venkatachala, pp. 67–68, figs. 1, 21.

Description. Monosaccate, elliptical in transverse plane, body elliptical to oval in outline. Monolete suture parallel to long axis, one-half of body length, usually splitting at maturity to form gaping fissure extending entire length of body. Bladder intrareticulate,

EXPLANATION OF PLATE 65

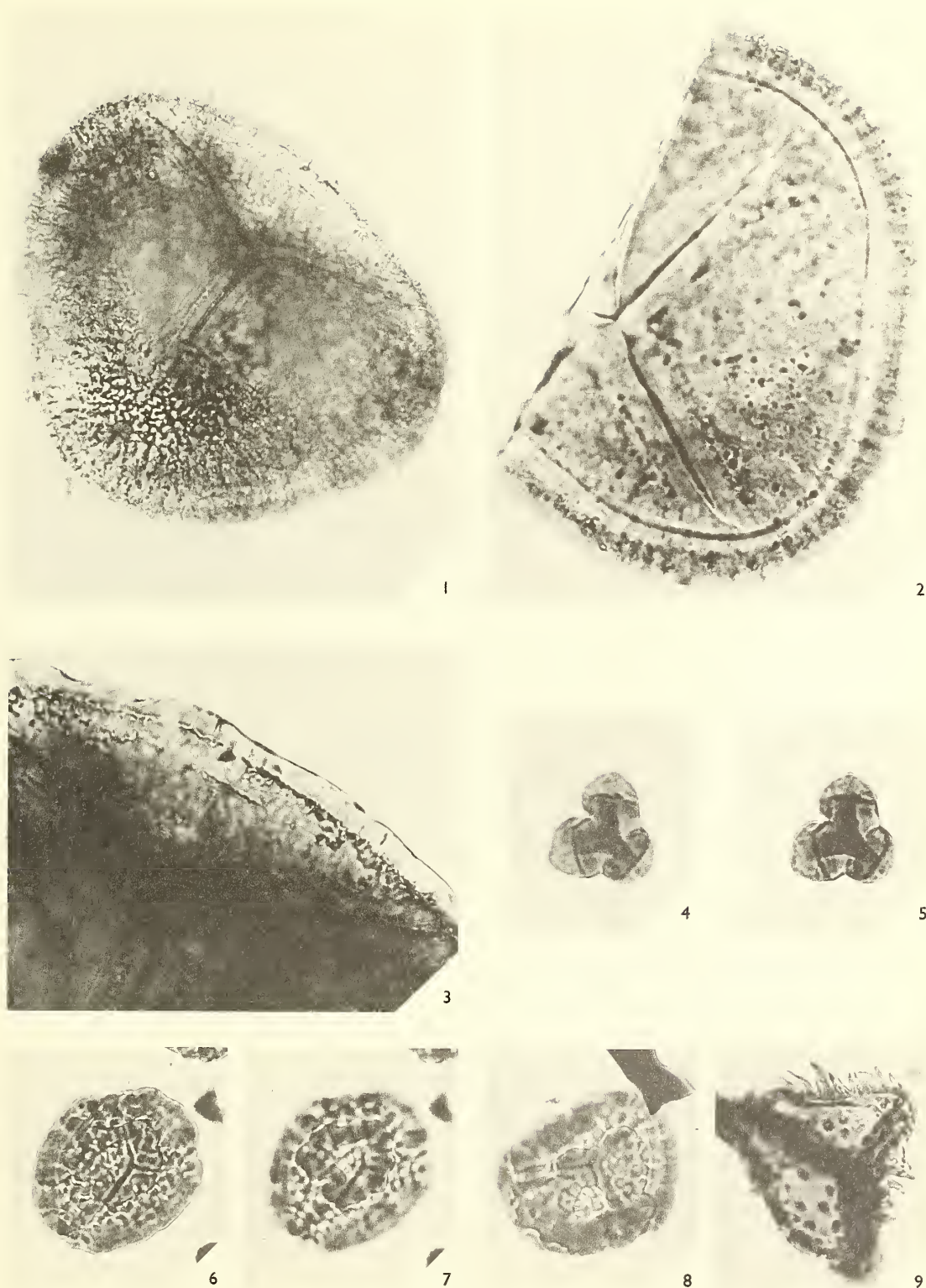
All figures $\times$ 500 unless otherwise indicated.

Figs. 1–3. *Hadrohercos stereon* sp. nov. 1, Holotype. Proximal surface; Slide O3V16–10 (2), location 23.5 $\times$ 114 (Ref. 53 $\times$ 117.7). 2, Wall detail; $\times$ 750. Slide O3V16–3 (6), location 41 $\times$ 125 (Ref. 33 $\times$ 117.9). 3, Wall detail; $\times$ 750. Slide O3V16–10 (2), location 23.5 $\times$ 114 (Ref. 53 $\times$ 117.7).

Figs. 4, 5. *Tantillus triquetrus* sp. nov. Holotype. Distal surface; $\times$ 750. Slide O3V16–11 (6), location 40.8 $\times$ 110.1 (Ref. 31.7 $\times$ 116.9).

Figs. 6–8. *Nexuosisporites contus* sp. nov. 6, Holotype. Proximal surface; Slide O3V16–11 (6), location 48.5 $\times$ 125.5 (Ref. 31.7 $\times$ 116.9). 7, Distal surface; Slide O3V16–11 (6), location 48.5 $\times$ 125.5 (Ref. 31.7 $\times$ 116.9). 8, Distal surface; Slide O3V16–11 (6), location 49.5 $\times$ 106.5 (Ref. 31.7 $\times$ 116.9).

Fig. 9. *Diatomozonotriletes* sp. Proximal surface; Slide O3V16–7 (2), location 24.5 $\times$ 116 (Ref. 31.5 $\times$ 116.8).



covering distal side of body, proximal body surface free of bladder attachment. Body marked by conspicuous distal folds, probably compressional, elliptical or biconvex in outline and oriented perpendicular to the monolete fissure. Another series of folds not so conspicuous and appearing to develop first, are formed along the margin of the central body. Central spore body itself is laevigate.

Dimensions. (50 specimens.) Over-all size $100 \times 137 \mu$ to $145 \times 200 \mu$. Body $70\text{--}72 \mu$ to $102 \times 108 \mu$.

Discussion. As with most fossil species, there are a number of variations evident in a study of large numbers. The conspicuous, characteristic lateral split is evidently a feature of development and subsequent compression. Excellently preserved specimens were observed with the suture intact and the lateral slit not yet developed. Similarly, in a few specimens, the distal folds across the suture are not formed or are only slightly developed in those specimens in which the full opening has not developed. In these instances however, the first series of folds about the margin of the central body are already evident.

Genus CYSTOPTYCHUS gen. nov.

Type species. *C. velatus* sp. nov.

Diagnosis. Spores monosaccate, radial, trilete; body circular to irregularly subcircular. Distinct central body surrounded by thin, flexuous bladder, which is characteristically folded obliquely to one side. Laesurae distinct, simple, straight, extending nearly to body margin; germinal apertures usually breached.

Cystoptychus velatus sp. nov.

Plate 63, fig. 5

Diagnosis. Monosaccate, trilete; spore body circular to irregularly subcircular. Laesurae straight, simple, $20\text{--}34 \mu$ long, extending nearly to body margin. Trilete area characteristically gaped open, forming triangular opening with dimensions $30 \times 40 \mu$ to $35 \times 55 \mu$. Thin, flexuous bladder entirely surrounding spore body and characteristically folded obliquely to one side. Bladder insertion at body equator and width up to 45μ . Spore body laevigate, wall 2μ thick, bladder minutely granulose.

Dimensions. (25 specimens.) Diameter of body $55\text{--}76 \mu$.

Holotype. Slide O3V16-9 (5). Location 30.2×115 (Ref. 32.4×118.6).

Description. Holotype body $70 \times 75 \mu$; body laevigate, wall 2μ thick; bladder minutely granulose, laterally compressed, extending 15μ beyond periphery of body. Trilete rent to form triangular opening $35 \times 55 \mu$.

Discussion. The asymmetrical appearance produced by the inclination of the bladder to fold in one direction, and the triangular breach or rent in the wall as a result of the open trilete, are the main distinguishing characters. Very rarely was a specimen observed with the bladder visible about the entire body periphery. The actual insertion of the thin bladder upon the body was difficult to ascertain. However, the orientation of the bladder to one side is not fortuitous but probably due to an oblique angle of insertion upon the body. This was never definitely observed, but fully 95 per cent. of the specimens had

the asymmetrical form shown in Plate 63, fig. 5. Similarly, at least 95 per cent. had the breached germinal opening. There is a superficial resemblance to *Auroraspora*, but in addition to the bladder insertion and the breached trilete, the body size is significantly greater than in *Auroraspora*, the ratio of body diameter to bladder width is appreciably less in *Cystoptychus*, and the bladder insertion on the body is much more pronounced in *Cystoptychus*.

ADDITIONAL SPRINGER TAXA

As is the case in most studies of the scope of this one, a number of unresolved problems remain. In many instances the authors have used their own judgement in evaluating the importance of a spore, and accordingly some representatives have been omitted. This is especially true of the *Granulatisporites* group where taxonomy is confused and morphological characteristics almost nonexistent. The majority of the spores probably assignable to this taxon from the Springer are omitted, but these and other taxa will receive further study should future developments in palynology render it advisable. Several identifiable entities were also observed but not treated formally because of poor preservation and/or insufficient specimens. Several of these are illustrated on Plates 65 and 66. Prominent among these is *Florinites volans* (Pl. 66, fig. 2), which was definitely identified but represented by only three specimens.

The zonate microspores referable to *Simozonotriletes* and *Murospora* are rare in the Springer, but a few were observed. Considerable disagreement still exists on the nomenclatural status of these genera, even though Playford (1962) has established a synonymy. In view of the still unsatisfactory taxonomy, both names are provisionally retained. Too few specimens were encountered in the Springer to allow any adequate interpretation. The specimen figured on Plate 66, fig. 8 is definitely assignable to *Murospora aurita* (Waltz) Playford 1962. The specimens on Plate 66, figs. 9, 10 are assignable to *Simozonotriletes* (*sensu* Sullivan 1958) and also exhibit the morphological variations he demonstrated in his nomenclatural treatment.

EXPLANATION OF PLATE 66

All figures $\times 500$ unless otherwise indicated.

Fig. 1. *Potonieisporites elegans* (Wilson and Kosanke) Wilson and Venkatachala 1964. Proximal surface; Slide O3V16-3 (5), location 24×110.8 (Ref. 33.7×118).

Fig. 2. *Florinites volans* (Loose) Potonié and Kremp 1955. Proximal surface; Slide O3V16-4 (R-1), location 34×120 (Ref. 32.3×118.7).

Fig. 3. Cellular sporangium. Slide O3V16-11 (7), location 29×110.9 (Ref. 31.9×117.9).

Fig. 4. Unknown spore. Proximal surface; Slide O3V16-9 (R-1), location 47×129 (Ref. 32.4×118.6).

Fig. 5. *Raistrickia* sp. Proximal surface; Slide O3V16-13 (A-2), location 36×116 (Ref. 32.2×115.5).

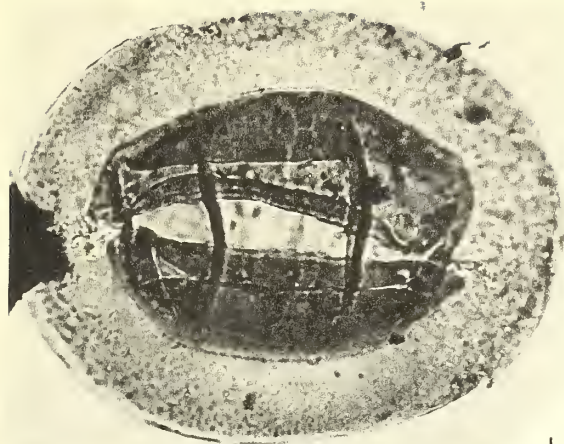
Fig. 6. *Alatisporites* sp. Showing six wings; Slide O3V17-7 (1), location 25×108.5 (Ref. 32×118).

Fig. 7. *Granulatisporites* sp. Proximal surface; Slide O3V16-4 (R-1), location 21.2×124.5 (Ref. 32.3×118.7).

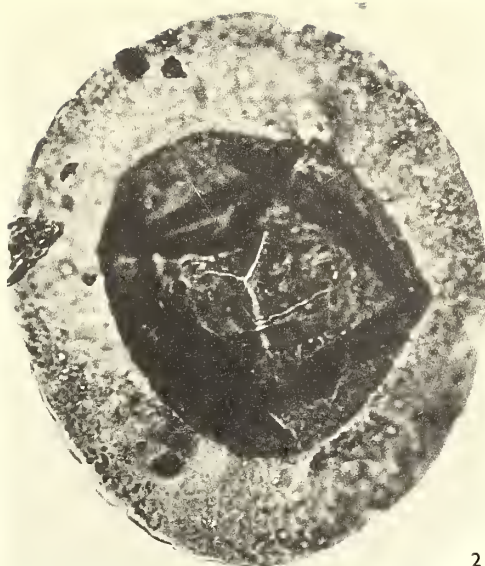
Fig. 8. *Murospora aurita* (Waltz) Playford 1962. Proximal surface; Slide O3V16-6 (2), location 45×109 (Ref. 33×117.8).

Figs. 9, 10. *Simozonotriletes* sp. 9, Distal surface; Slide O3V16-10 (A-2), location 18.6×107 (Ref. 30×117.6). 10, Proximal surface; Slide O3V16-10 (A-2), location 48×121 (Ref. 30×117.6).

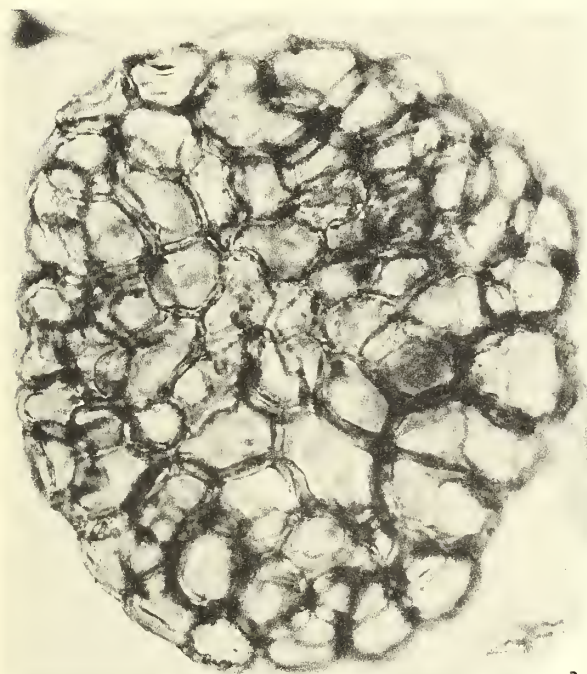
Fig. 11. *Procoronaspora fasciculata* Love 1960. Proximal surface; Slide O3V16-3 (1), location 25×127 (Ref. 33×117.1).



1



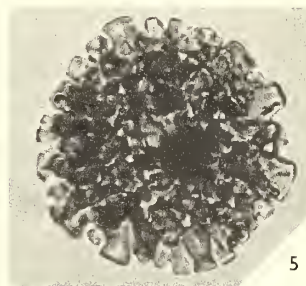
2



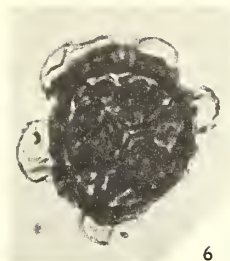
3



4



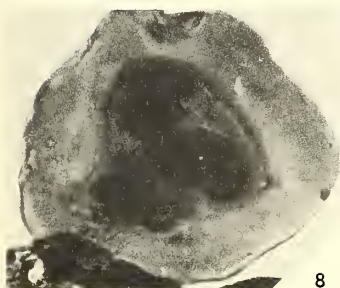
5



6



7



8



9



10



11

REFERENCES SPORE SPECIES	MISSISSIPPIAN												PENNSYLVANIAN						SURFACE SPRINGER				
	KINDER - HOOK		OSAGE	MERA- MEC	CHESTER				MORROW			ATOKA											
	TOURNAISIAN			MIDDLE VISEAN	UPPER VISEAN			NAMURIAN		WESTPHAL.			WEST- PHAL.										
								A	B & C	A			B										
	PLAYFORD 1962 & 1963	HACQUEBARD 1957	PLAYFORD 1964	SULLIVAN 1964 b	PLAYFORD 1962 & 1963	LDVE 1960	WIGGINS 1962	STAPLIN 1960	H. S. & M. 1955 b	SULLIVAN 1964 a	SULL. & MARSH 1966	HACO & BARSS 1957	BUTT. & WILL. 1958	NEVES 1961	NEVES 1961	NEVES 1958	ARTUZ 1957	SULLIVAN 1964 a		KOSANKE 1950	GUENNEL 1958	KOSANKE 1950	GUENNEL 1958
LOPHOTRILETES CONIFERUS	•																						
KNOXISPORITES HEDERATUS	•			•																			
LEIOTRILETES ORNATUS	•				•																		
L SUBINTORTUS VAR. ROTUNOATUS	•																						
CONVOLUTISPORA CRASSA	•				•																		
STENOZONOTRILETES SPETCANOUS	•				•																		
DENSOSPORITES VARIABILIS	•				•								•										
PEROTRILETES PERINATUS	•			•																			
CONVOLUTISPORA VERMIFORMIS	•		•																				
ENDOSPORITES MICROMANIFESTUS	•	•	•			•					•												
CYCLOGRANISPORITES LASIUS	•				•																		
PUNCTATISPORITES SOLIUS		•																					
PUNCTATISPORITES IRRASUS		•																					
GRANOISPORA ECHINATA		•																					
LYCOSPORA UBER		•				•		•			•	•											
DENSOSPORITES ACULEATUS			•																				
KNOXISPORITES TRIRAOIATUS				•	•	•			•								•						
RETICULATISPORITES PELTATUS					•	•		•															
ANAPICULATISPORITES CONCINNUS					•	•		•															
DENSOSPORITES RARISPINOSUS					•	•																	
DENSOSPORITES IRREGULARIS					•	•						•											
WALTZISPORA SAGITTATA					•	•																	
SCHULZOSPORA RARA					•	•																	
LEIOTRILETES TUMIDUS					•	•																	
LYCOSPORA NOCTUINA					•	•					•	•											
CONVOLUTISPORA MELLITA					•	•				•	•	•											
KNOXISPORITES STEPHANEPHORUS					•	•				•	•	•											
CONVOLUTISPORA FLORIDA					•	•																	
KNOXISPORITES CORPOREUS					•	•																	
PROPRISPORITES RUGOSUS					•	•																	
CIRRATRIRAOITES SATURNI					•	•																	
SAVITRISPORITES NUX					•	•																	
TRIPARTITES VETUSTUS					•	•																	
KNOXISPORITES OISSIOIUS					•	•																	
SECARISPORITES REMOTUS					•	•																	
DICTYOTRILETES PACTILIS					•	•																	
DICTYOTRILETES CLATRIFORMIS					•	•																	
CRASSISPORA KOSANKEI'					•	•																	
SPENCERISPORITES RADIATUS					•	•																	
ROTASPORA FRACTA					•	•																	
GRANOISPORA SPINOSA					•	•																	
LYCOSPORA NITIDA					•	•																	
AURORASPORA SOLISORTUS					•	•																	
GRANULATISPORITES TUBERCULATUS					•	•																	
CONVOLUTISPORA VENUSTA					•	•																	
GRANULATISPORITES POLITUS					•	•																	
LYCOSPORA PSEUDOANNULATA					•	•																	
GRANULATISPORITES PALLIDUS					•	•																	
TRICIOARISPORITES CF BALTEOLUS					•	•																	
SIMOZONOTRILETES INTORTUS					•	•																	
DICTYOTRILETES INSCULPTUS					•	•																	
MOOREISPORITES TRIGALLERUS					•	•																	
FLORINITES VISENDUS					•	•																	
PROPRISPORITES LAEVIGATUS					•	•																	
REINSCHOSPORA SPECIOSA					•	•																	
LOPHOTRILETES LABIATUS					•	•																	
LAEVIGATOSPORITES OVALIS					•	•																	
CALAMOSPORA PARVA					•	•																	
GRANULATISPORITES SPINOSUS					•	•																	
LYCOSPORA BREVIJUGA					•	•																	

TABLE 1

Comparison of the Springer spore assemblage with other recorded spore assemblages.

OCCURRENCE SPECIES	MISSISSIPPIAN		PENNSYLVANIAN
	GODDARD	SPRINGER	MORROW
DICTYOTRILETES BIRETICULATUS			_____
RETICULATASPORITES FACETUS			_____
VESTISPORA PROFUNDA			_____
WILSONITES VESICATUS			_____
FLORINITES ANTIQVUS			
MOOREISPORITES INUSITATUS			_____
REINSCHOSPORA BELLITAS			_____
CONVOLUTISPORA TESSELLATA			_____
OENOSPORITES ANNULATUS			_____
ENOOSPORITES FORMOSUS			_____
FLORINITES VISENOUS			
LAEVIGATOSPORITES OVALIS			
POTONIEISPORITES ELEGANS			
SAVITRISPORITES NUX			
KNOXISPORITES OISSIOIUS			
CIRRATRIRADITES SATURNI			
CONVOLUTISPORA FLORIDA			
KNOXISPORITES TRIANGULATUS			
KNOXISPORITES STEPHANEPHORUS			
LYCOSPORA PSEUDOANNULATA			
OENOSPORITES VELATUS		_____	
PUNCTATISPORITES VALIUS			
RETICULATASPORITES LACUNOSUS			
REINSCHOSPORA SPECIOSA			
PROPRISPORITES LAEVIGATUS			
CYSTOPTYCHUS VELATUS			
KNOXISPORITES INCONSPICUUS			
CIRRATRIRADITES RUSTICUS		_____	
LYCOSPORA NITIOA			
LYCOSPORA NOCTUINA			
ROTASPORA FRACTA			
AURORASPORA SOLISORTUS			
TRIPARTITES VETUSTUS			
RETICULATISPORITES PELTATUS			
PROPRISPORITES RUGOSUS			
CONVOLUTISPORA VERMIFORMIS			
OENOSPORITES IRREGULARIS			
SCHULZOSPORA RARA			
VELAMISPORITES VERMICULATUS			
LOPHOTRILETES LABIATUS			
SCUTULUM PUSILLUM			
PUNCTATISPORITES HETEROFILIFERUS			
ENOOSPORITES MICROMANIFESTUS			
GRANOSPORA SPINOSA		_____	
PTERORETIS PRIMUS			
REINSCHOSPORA UBERTUS			
MOOREISPORITES FUSTIS			
LOPHOZONOTRILETES TRIANGULATUS			

TABLE 2

The ranges of key spores illustrated are based upon the occurrence of spores in the surface Goddard and Springer formations of Johnston County, Oklahoma at the Goddard Ranch locality. The Morrow occurrences are the results of subsurface studies in the Anadarko Basin and from the examination of surface samples from the Morrow type area of Arkansas.

Sullivan and Marshall (1966) have considered *Procoronaspora* as a junior synonym of *Rotaspora*, making retention of *Procoronaspora* unnecessary. Their basis for this is the possession of a cingulum which is wider interradially than at the apices. However, a few specimens have been observed in the Springer (Pl. 66, fig. 11), which possess an

incipient corona and no definable cingulum. These compare most closely with *Procoronaspora fasciculata* Love (1960). Sullivan and Marshall (1966) may be justified in their interpretation of *P. ambigua* as *Rotaspora*, but it appears quite likely that the specimens of Love and those from the Springer cannot be assigned to *Rotaspora*. Sullivan and Marshall (1966) did place Love's species in their new genus *Tricidarisporites*, but we have chosen to reject this assignment and question whether their illustrated specimens are the same as that of Love. Since Sullivan and Marshall's synonymy involved the holotype of *Procoronaspora*, there is no depository for our specimens. We lack sufficient material to make an adequate study, but restudy of *P. fasciculata* should provide clarification as to whether assignment to *Rotaspora* is warranted or if a new taxon is required.

Also observed in the Springer from samples O3V16-6 and O3V16-14, but not illustrated, were specimens assignable to the genus *Tricidarisporites* described by Sullivan and Marshall (1966) and probably referable to their species *T. balteolus*.

The specimen figured on Plate 54, fig. 4 offers the possibility of a definable taxon because of its unusual morphology, but insufficient specimens were observed for formal treatment.

The cellular mass illustrated on Plate 66, fig. 3 was very conspicuous throughout the Springer section and was especially common in sample O3V16-11. It is definitely a sporangial structure, and occasionally small trilete spores were observed associated with the cells, but these spores were not treated separately in this study. Poorly preserved specimens of *Spencerisporites* were also noted; the extreme rarity of this genus was somewhat unexpected since we have often observed it in considerable numbers from older sediments, and frequently it is abundant in lower Pennsylvanian strata.

EVALUATION OF THE PALYNOLOGY OF THE SPRINGER

Our initial interpretation of the Springer formation was one of a transitional microflora, ranging from predominantly Mississippian in the lower Springer to Pennsylvanian in the upper part of the formation. However, our study has not borne out all early expectations. The Springer formation does have a transitional spore flora in the qualitative sense as illustrated in Table 1, for it does contain spores representative of lower Mississippian (Tournaisian) through the lower Pennsylvanian (Westphalian B). Table 2 demonstrates that the Springer formation in the study area contains several spore species commonly associated only with Pennsylvanian age sediments, as well as some characteristic only of the Mississippian. It also has a number of longer ranged species, which extend without interruption from the upper Mississippian into the lower Pennsylvanian. However, quantitatively the Springer is not as transitional as it is simply a mixed microflora, and the anticipated gradation from predominantly Mississippian in the lower Springer to a predominantly Pennsylvanian in the upper Springer did not materialize. Expectations were that the lower Springer would be entirely Mississippian in character, with the Mississippian spores progressively decreasing both quantitatively and qualitatively upsection and a subsequent quantitative and qualitative increase in Pennsylvanian representatives to a completely Pennsylvanian population in the upper Springer. There is, in actuality, an erratic occurrence of predominantly Pennsylvanian or predominantly Mississippian population throughout the entire Springer section (Table 4). At times there is a considerable percentage of both Mississippian and Pennsylvanian

SAMPLE SPORE SPECIES	03V16-1	03V16-3	03V16-4	03V16-5	03V16-6	03V16-7	03V16-8	03V16-9	03V16-10	03V16-11	03V16-12	03V16-13	03V16-14	03V17-1	03V17-2	03V17-4	03V17-5	03V17-7	03V18-1	03V19-1
*CHAETOSPHAERITES POLLENISIMILIS	.5	.5	.5		.5	.5	.5													
*LEIOTRILETES ORNATUS		.5									.5	.5		.5						
*LEIOTRILETES SUBINTORTUS VAR ROTUNGATUS								15						.5	15					
*LEIOTRILETES TUMIDUS	5					5	5			5	.5									
PUNCTATISPORITES OIVARICATUS		15		.5																
PUNCTATISPORITES FLEXUOSUS															.5					
PUNCTATISPORITES HETEROFILIFERUS	10	10.0	5.5	3.5	5.5	25	9.0	9.5	7.0		.5				70		130			
PUNCTATISPORITES INCOMPTUS	.5							5	10			.5								
PUNCTATISPORITES IRRASUS	10		.5				.5													
*PUNCTATISPORITES SOLIUS	20	5		15	.5	30	10	20	40	.5				.5	10			10		10
PUNCTATISPORITES TRIFIDUS		.5		.5				5	15			.5								
PUNCTATISPORITES VALIUS	40	10	10	3.5	3.5	25	35	.5	85	20	10	.5	15	.5	30		15	10	.5	100
CALAMOSPORA CF. HARTUNGIANA	20	45	45	15	35	.5	45	45	20	25	10	15	25	30	30		80	90	25	
CALAMOSPORA CF. PARVA	20	45	45	25	20	10	15	30	.5	20	10	.5	15	30			35	30	10	
*WALTZISPOA SAGITTATA				10				15		5	5									
GULISPORITES INCOMPTUS	.5		.5	20	15	10	.5		25	.5										40
HAORHERCOS STERON				.5																
*CYCLOGRANISPORITES LASIUS	15	20	10	20			.5		25	15	10	.5	10	20	10		5	15	15	
GRANULATISPORITES CF. PALLIUS	105	90	45	5.5	50	25	25	25	70	85	45	45	10	50	90		5		35	
GRANULATISPORITES POLITUS	5	15	5	5									.5							
GRANULATISPORITES SPINOSUS	25	15		10	10				10		.5		.5				.5		.5	
GRANULATISPORITES TUBERCULATUS	25	25	10	10	.5		15	.5		25	5	5	.5	15	25				10	
*LOPHOTRILETES CONIFERUS		.5										.5			.5					
LOPHOTRILETES LABIATUS																				
LOPHOTRILETES OBTUSUS	15	10		10	.5				25	15	.5		.5	.5	15					
*ANAPICULATISPORITES CONCINNUS	.5	.5																		
RAISTRICKIA VULGATA								.5					.5	.5						
IBRAHIMISPORES SENTUS																				
SPINOZONOTRILETES PROCINCTUS		.5		10	.5				25											
MOOREISPORITES LUCIUS												.5								
MOOREISPORITES TRIGALLERUS																				
CYCLOBACULISPORITES GRANOIVERRUCOSUS	10	5		.5	15	5	10		5				15							
GRANDISPOA ECHINATA																				
*GRANDISPOA SPINOSA					10		.5													
CONVOLUTISPOA CRASSA																				
CONVOLUTISPOA FLORIDA	10	15		15	5	.5			15					10	25			10		10
CONVOLUTISPOA LEPIDA																				
*CONVOLUTISPOA MELLITA			.5		.5	.5	.5						.5	10	25					
CONVOLUTISPOA SCULPTILIS																				
CONVOLUTISPOA SUPERFICIALIS				.5			.5													
CONVOLUTISPOA VENUSTA						5			10				.5							
CONVOLUTISPOA VERMIFORMIS																				
*OICTYOTRILETES CLATRIFORMIS	20	15	.5				.5	5	5	20	15	10	15		12.5					
*OICTYOTRILETES PACTILIS	30		.5				.5	5			.5									
OICTYOTRILETES INSCULPTUS																				
RETICULATISPORITES DECORATUS				.5																
*RETICULATISPORITES PELTATUS					.5				.5										.5	
FOVEOSPORITES FUTILIS	10	5										.5								
SECARISPORITES REMOTUS	5		.5		5		.5	15	5					10						
RETICULATISPORITES LACUNOSUS		.5						5	5									.5		10
PEROTRILETES PERINATUS		.5	.5	.5										.5						
*VELAMISPORITES DESCRETUS			.5	.5																
VELAMISPORITES VERMICULATUS				.5					.5											
TRIPARTITES OUBITALIS																				
*TRIPARTITES VETUSTUS						.5			.5					.5	20					
AHRENSISPORITES IRRORATUS																				
SCUTULUM PUSILLUM											.5									
TANTILLUS TRIQUETRUS	10	10						5		5		.5	.5	.5	.5				5	
LYCOSPOA BREVIJUGA		45	10	5	10		.5	55		15		20	30	10						
*LYCOSPOA NITIOA	10	.5																		.5
*LYCOSPOA NOCTUINA	.5	35	125	75	50	45	90	75		305	110	165	85	60			.5		25	
LYCOSPOA PSEUDOANNULATA	30	110	205	165	175	205	215	135	30	95	545	440	515	110	85		20	30	425	580
*LYCOSPOA UBER						20		25	10	15	15	60								
*ROTASPOA FRACATA							.5													
SIMOZONOTRILETES INTORTUS																				
DENSOSPORITES VELATUS													.5	.5			65	85		

SAMPLE SPORE SPECIES	03V16-1	03V16-3	03V16-4	03V16-5	03V16-6	03V16-7	03V16-8	03V16-9	03V16-10	03V16-11	03V16-12	03V16-13	03V16-14	03V17-1	03V17-2	03V17-4	03V17-5	03V17-7	03V18-1	03V19-1
*OENSOSPORITES ACULEATUS		●	.5		●	●		.5	5			●		.5						1.0
OENSOSPORITES HISPIOUS	1.0	10.5	2.5	5.5	12.0	6.5	1.5	●	1.0	2.0	5.0	9.5		.5				5	6.5	2.0
*OENSOSPORITES IRREGULARIS		●	1.5	1.5	1.0	3.0		.5				●	.5	●					.5	●
OENSOSPORITES RARISPINOSUS	.5	.5		.5	1.0	.5	.5	3.0	●			1.5	.5	3.0						
*OENSOSPORITES VARIABILIS			1.0	1.5	4.0	4.5	2.5	●		.5	.5	.5	2.5	1.0					1.5	1.0
DENSOSPORITES OISSIMILIS		●	●	●	.5	1.0	1.0	.5		.5	1.0		●						5.0	1.0
KNOXISPORITES CORPOREUS	●	●					●		●	.5										1.0
*KNOXISPORITES OISSIOIUS		●	●	.5				●				●		●	●					
*KNOXISPORITES HEDERATUS		.5			.5		.5	1.5	1.0	.5				.5	.5					
KNOXISPORITES INCONSPICUUS	●	.5			●		.5	1.5			.5	●		●						
*KNOXISPORITES TRIADAIATUS	1.0	.5		●		5	.5	●	.5	.5		●	●	●						●
*KNOXISPORITES STEPHANEPHORUS	.5	●	●	●			1.5	.5		●	.5	●	●	●	1.5					
NEXUOSISPORITES COMTUS	●					5			●						●					
*STENOZONOTRILETES CF. SPETCANOUS		●	●	.5	.5		●	.5	.5			●	.5					●		
CRASSISPOA KOSANKEI'		.5	.5	1.5	1.0	1.0	1.5	1.5	●	.5	●	.5	.5	2.0	2.5		10.5	6.5		
CRISTATISPORITES INOIGNABUNOUS		●	.5	.5	1.0		.5	.5		.5	.5	●		●						
CINCTURASPORITES MINIMUS				●				.5	●		.5									
CINCTURASPORITES MAGNUS				.5	●		●	●						●	.5					
TROCHOSPOA MASTOSPINOZA			.5	.5			.5	●		●			.5							
SAVITRISPORITES NUX	1.0	.5	●	●	.5	.5	.5	.5	●			●	.5	1.0	7.0	●		●	1.5	
CIRRATRIRADITES LEPTOMARGINATUS	●	●	.5	.5				●		.5				●						
CIRRATRIRAOITES RUSTICUS		●	3.0	1.5	●	.5	.5													
CIRRATRIRAOITES SATURNI	●	5	.5	.5	1.5	2.5	1.5	.5	2.0	●		●	.5	1.0	.5					1.0
REINSCHOSPOA SPECIOSA			●	●	●		●	●				●								
PROPRISPORITES RUGOSUS							●			●										
*PROPRISPORITES LAEVIGATUS	●	.5	●					.5	2.5	●		●								2.0
HYMENOSPOA CAPERATA	.5	.5	●	.5	.5		●	●	●				5	1.0	1.5	●				
LAEVIGATOSPORITES OVALIS		●			●		●	●	●			●		1.0						
MONOLETES OVATUS		.5	●	2.5	3.5	.5	●	1.5	2.5	.5		.5	5	6.0	1.5	●	1.5	23.0	●	
MONOLETES SP.				.5			●	.5	.5			●		●						
*ENDOSPORITES MICROMANIFESTUS		.5	●	●				.5	.5					1.0						
*SCHULZOSPOA RARA		.5	●		●			.5	●			●	●	●	.5		1.5	5		
FLORINITES GUTTATUS	2.5		●						5.0	●		●		●				1.0	1.0	
FLORINITES VISENOUS	11.5	●	.5				.5	●	3.0	.5	●	●	22.0	6.0	●	3.5	11.5	3.0	2.0	
*AUORASPOA SOLISORTUS	1.0	.5	.5	.5	●		.5	.5	1.0	.5		●		●	1.0		●			
COSTATASCYCLUS CRENATUS		●	.5					.5	1.0	1.0		●	●		.5					
POTONIEISPORITES ELEGANS	1.0	1.5	1.5	.5			1.0	●	3.0	4.5	1.0	.5	.5	.5		●	●	2.0	1.5	5.0
CYSTOPTYCHUS VELATUS	5.0	8.5	●	2.0	1.0		●	1.0	.5			●	●	●		.5				

TABLE 3

Spore distribution in the Springer formation from samples suitable for quantitative specific estimation. Constituent species are listed as percentages based upon individual counts of 300 specimens. Species observed in a particular sample but not occurring in actual count are indicated by '●'. Species utilized in compiling composite percentages in Table 4 are indicated by '*'.

representatives together in samples as in O3V16-1, O3V16-3, O3V16-10, and O3V17-1. On occasion the assemblage is dominated by either Pennsylvanian alone or only Mississippian as in O3V16-4 through O3V16-9 which is largely Mississippian or O3V17-7 and O3V19-1 which is largely Pennsylvanian. It might be best said that the Springer represents a final transgressional facies of the Mississippian Goddard formation rather than being transitional. There are a number of spores observed to be restricted to the Springer formation, both in the surface area of interest and in the subsurface of the Anadarko Basin. Chief among these are *Densosporites velatus*, *Reticulatasporites lacunosus*, *Cystoptychus velatus*, *Cirratriradites rusticus*, and *Propriporites laevigatus*. However, valuable though they may be, they constitute such a numerical minority that

the over-all features of the assemblage must be considered in each sample and the mixed nature of the 'population' enters into any analysis.

The formation is characterized by the occurrence of a number of genera usually regarded as restricted to the Mississippian and considered to be reliable Mississippian age indicators. Among these are *Auroraspora*, *Rotaspora*, *Propriisporites*, and *Tripartites*. Similarly, such species as *Lycospora noctuina*, *L. nitida*, *Reticulatisporites peltatus*, and *Densosporites irregularis* also regarded as Mississippian are present. A number of other genera considered to be at least predominantly Mississippian are also recorded; *Schulzospora* is perhaps the principal one, while *Cincturasporites*, *Velamisporites*, and *Waltzisporea* may be included within this category. On the other hand, a number of spores usually regarded as Pennsylvanian in range occur throughout the Springer, often in large numbers and frequently in association with the Mississippian representatives. The monosaccate genera *Florinites* and *Potonieisporites* and the monoete *Laevigatisporites* are perhaps the most striking examples. The saccate genera also best illustrate the absence of a transitional microflora, for two of the highest percentage occurrences of saccate forms are in the lowermost and uppermost samples (Table 4). In both samples the principal saccate representative is *Florinites visendus* (Table 3). The presence of the saccate genera is not unique, and Neves (1961, p. 276) recorded *Florinites elegans*, *F. similis*, and *F. visendus* from the Namurian A, the first records of these monosaccate grains from this age deposit. The saccate genera constitute one of the most noticeable differences between the Goddard and the Springer. In his Goddard investigation, Wiggins (1962) recorded only ten or fifteen saccate specimens in a survey of 600 slides.

Although the Springer is difficult to characterize in its entirety on the basis of a distinct entity or even assemblage, it does have a number of noteworthy trends (Tables 3, 4). Over-all the lower Springer is marked by the large numbers of *Punctatisporites*, and the lowermost Springer (O3V16-1, 3) has 5.0-8.5 per cent. of *Cystoptychus*, which is rare in the remainder of the formation. The middle Springer is distinguishable by the large numbers of *Lycospora noctuina*. In the upper Springer *Densosporites velatus* does not appear until O3V16-13 and ranges from 6.5-8.5 per cent. in the upper Springer. Although *Monoletes ovatus* is present throughout the section in small numbers, it is a conspicuous representative in the upper Springer where it composes 23 per cent. of sample O3V17-7. Several genera are completely absent from the upper Springer, and most notable among these and not recorded above O3V17-2 are *Ibrahimisporites*, *Mooreisporites*, *Grandispora*, *Velauisporites*, *Rotaspora*, *Nexuosisporites*, and *Cincturasporites*. However, they usually constitute such a small part quantitatively that their presence or absence is often difficult to detect.

Relatively few significant trends are evident in the distribution of genera, and *Lycospora* and the saccate genera are the most noteworthy (Table 4). The species included in the composite saccate grouping of Table 4 are *Florinites guttatus*, *F. visendus*, *Costatascychus crenatus*, *Cystoptychus velatus*, and *Potonieisporites elegans*. Both spore groups demonstrate changes in crossing the sandstone intervals. At the Overbrook sand the assemblage is marked by the near disappearance of *Lycospora* statistically, but with a considerable increase in the saccate spores, particularly *Florinites* and *Potonieisporites*. A somewhat similar trend is also present at the Lake Ardmore sand. It might also be significant that, whereas the percentage of *Lycospora* as a whole decreases in crossing the sandstone intervals, in both instances *Lycospora noctuina* disappears completely

qualitatively and quantitatively. These patterns of distribution tend to indicate the possibility of an additional sandstone section in the covered interval between samples O3V16-14 and O3V17-1. The over-all *Lycospora* population and the saccate genera demonstrate trends comparable to those present in crossing the Overbrook and Lake Ardmore sandstones. However, *Lycospora noctuina* does not substantiate this since it is present in fair numbers. There is the possibility that shales immediately adjacent to a covered section were not sampled. However, field examination of the exposure did not indicate the existence of such a sand, and the sole evidence is based upon the pattern of general spore populations.

SAMPLE SPORES	O3V16-1	O3V16-3	O3V16-4	O3V16-5	O3V16-6	O3V16-7	O3V16-8	O3V16-9	O3V16-10	O3V16-11	O3V16-12	O3V16-13	O3V16-14	O3V17-1	O3V17-2	O3V17-5	O3V17-7	O3V18-1	O3V19-1
LYCOSPORA	4.5	19.5	34.0	24.5	23.5	27.0	31.0	29.0	4.0	43.0	67.0	68.5	63.0	18.0	8.5	2.5	3.0	45.5	8.0
SACCATE	20.0	10.0	2.5	2.5	1.0	1.5	1.5	1.5	13.0	5.5	1.5	0.5	0.5	22.5	6.5	3.5	14.0	5.5	25.0
COMPOSITE 6 MISSISSIPPIAN	1.0	1.0	0.5	1.0	1.0	0.5	1.0	1.5	4.0	0.5	—	—	—	0.5	3.0	—	—	—	2.0
COMPOSITE 32 MISSISSIPPIAN	9.5	12.0	19.0	17.0	14.0	19.0	19.0	20.0	16.0	40.0	17.5	25.5	14.5	14.5	25.5	2.5	3.0	7.0	5.0

TABLE 4

Spore distribution of composite groupings of selected species from the Springer formation.

The lack of a well-defined gradation from Mississippian to Pennsylvanian is further demonstrated by the percentage occurrences of several Mississippian species. A composite group of six reliable Mississippian species in Table 4 shows the highest percentage occurrence to be only 4 per cent., near the middle of the section. In some samples these species are not even represented. The six species utilized are *Grandispora spinosa*, *Tripartites vetustus*, *Lycospora nitida*, *Rotaspora fracta*, *Proprisporites laevigatus*, and *Auroraspora solisortus*. A second evaluation was made grouping thirty-two species considered as predominantly Mississippian. These are each indicated by an asterisk in Table 3 and include the six species used in the previous discussion. Here, again, no gradational pattern was evident, and in truth the upper Springer has perhaps a slightly more Mississippian appearance than does the lower Springer. The percentage of Mississippian species is often affected by *Lycospora noctuina*, which sometimes occurs in sufficiently high numbers to obscure the other components.

It is admittedly difficult, when working with such assemblages as these, to identify them accurately since given samples may be Pennsylvanian or Mississippian in character. The Springer assemblages are probably ecologically influenced in deposition, and on occasion it could be impossible to place a sample in its proper place in the section. Floras such as the Springer are not unusual in megafossil studies, and Tschudy (1964) has cited what he terms as transitional floras in the Devonian-Mississippian, the Mississippian-Pennsylvanian, the Pennsylvanian-Permian, the Jurassic-Cretaceous, and the Cretaceous-Tertiary. He also noted that pollen and spore assemblages also demonstrate similar transitions.

Wilson (1964) has discussed the problem of recycling in the Springer of the Anadarko Basin, and his (1965) Ti Valley study is also described as containing recycled fossils. The authors are well aware of redeposition possibilities and of the presence of such processes in the Anadarko Basin and adjacent areas. The Springer has been regarded at times as being a mixture of Pennsylvanian spores and recycled Mississippian spores. However, there is no evidence for such an interpretation of the Springer in the area considered. The microfossils do not show the colour, stain, or preservational features utilized by Wilson (1964, 1965) in determining recycling. During a period of ten years this laboratory has made an extensive study of Morrow–Springer–Chester palynology throughout the Anadarko Basin subsurface, as well as many surface exposures in the south-western United States. Recycling such as Wilson described for the Springer (1964, p. 428) in the western Anadarko Basin has been observed on occasions, and we have established a detailed zonation of the Morrow formation based upon the presence of recycled Springer. However, it would not be realistic to expect the entire vast Anadarko Basin to be uniformly recycled, and most of the subsurface Springer compares with the surface populations treated in this study and reveals no evidence for recycling or stratigraphic leakage.

Location of types. The exact field position of specimens is noted in text and plate explanations as coordinates, in parentheses, followed by a reference point coordinate for each slide. Calibration was on a Leitz Ortholux microscope mechanical stage to tenths of millimetres, with horizontal (smaller) reading listed first. Traverse (1958, 1960) and Pierce (1959) have dealt in detail with methods of co-ordinate conversion used here. Type slides are filed in the Sun Oil Company Paleontological Collections, Richardson, Texas, U.S.A.

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CHLAMYDOPHYLLUM, IOWAPHYLLUM, AND SINOSPONGOPHYLLUM (RUGOSA) FROM THE DEVONIAN OF NEW SOUTH WALES

by D. L. STRUSZ

ABSTRACT. The new species *Chlamydophyllum minus* and *Iowaphyllum cabonnense* are described from the Lower Devonian Garra Formation of New South Wales. This is the first record of *Iowaphyllum* from Australia. *Sinospongophyllum tabulatum* Hill, known from the Devonian limestones of Mt. Etna and Silverwood, Queensland, is also recorded from the Garra Formation. The correlation of these limestones with the Garra Formation is discussed; it is concluded that the three are representatives of an Eastern Australian faunal association of probable Emsian, and possible Early Eifelian age.

THE Garra Formation is a calcareous sequence of Devonian age, which crops out in a meridional belt, some 60 miles long and 5 miles broad, in the Molong-Wellington region of the central western slopes of New South Wales. The stratigraphy and structure have already been described and summarized (Strusz 1963, 1965b).

The localities from which the fossils described herein were collected are given in an appendix; their approximate positions are shown on the accompanying geological map (text-fig. 1).

Abbreviations used in the following descriptions are as defined in Strusz (1965a). Repositories of specimens mentioned are indicated by the following prefixes: SU; Palaeontological collection, Department of Geology and Geophysics, University of Sydney. UQ; Palaeontological collection, Department of Geology, University of Queensland.

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SYSTEMATIC PALAEONTOLOGY

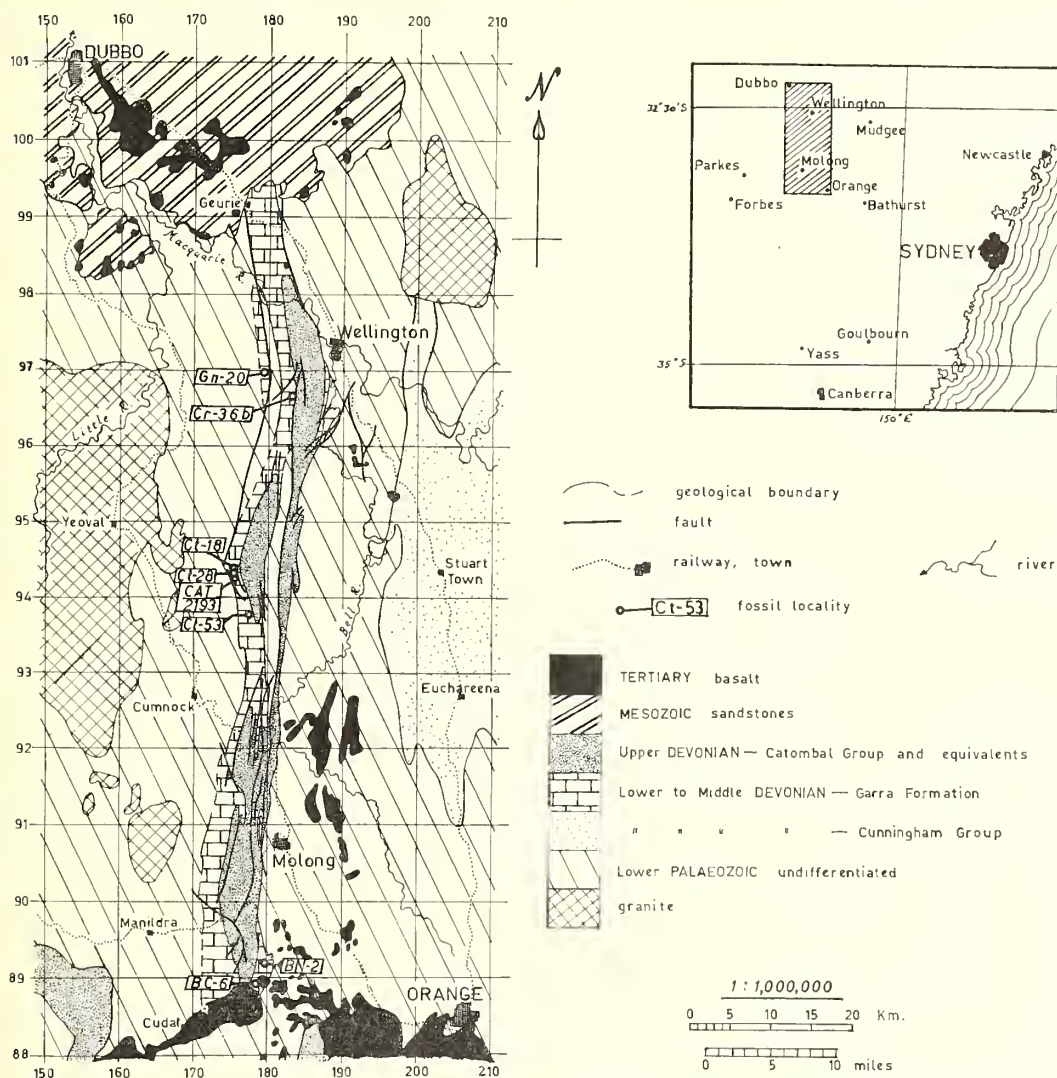
Family STREPTELASMATIDAE

Genus *Chlamydophyllum* Pořta 1902

Type species. *Chlamydophyllum obscurum* Pořta (1902, p. 136, pl. 114, fig. 2, pl. 115, figs. 2-5). Lower Devonian (f2), Koněprusy, Bohemia.

Diagnosis. Solitary coral, with a very wide septal stereozone from which dissepiments are lacking; major septa, thin or slightly dilated in tabularium, may unite at axis in proximal parts of corallite, and on tabular surfaces in distal parts, where they are amplexoid; axial lobes few and thickened.

Remarks. *Chlamydophyllum* is distinguished from the related Silurian solitary *Kodonophyllids* *Kodonophyllum* Wedekind 1927 and *Schlotheimophyllum* Smith 1945 principally in having amplexoid septa in the more distal parts of the corallite. *Schlotheimophyllum* is distinguished from *Kodonophyllum* by its distinctive patellate growth form.



TEXT-FIG. 1. Geological map of the Dubbo-Wellington-Molong-Orange region, showing the approximate positions of localities mentioned in the text. Inset shows the geographic location of the area under study.

The European species attributed to *Chlamydophyllum* (see Penecke 1894, p. 593; Le Maître 1934, p. 160; discussion in Hill 1940, p. 160) agree in growth form—cylindrical to irregularly ceratoid. A number of specimens have been described from Eurasia under the name *Zelophyllia* Soshkina 1952 (see Soshkina 1952, p. 74; Spasskiy 1955, p. 96;

1959, p. 29; 1960, p. 119; Besprozvannykh 1964, p. 58) and *Rhegmaphyllum* (see Soshkina 1937, p. 58—*tabulatum* only). They agree in external and internal structure with *C. obscurum*, save that the marginaria are rather narrow. Until the type species is re-studied (cf. Hill 1940, p. 160), the Eurasian species are best placed in *Chlamydo-phyllum*, as suggested by Soshkina (p. 309 in Orlov 1962). The Australian specimens so far recorded have corallites which tend towards a patellate form—they are further discussed below.

Stumm (1964, p. 25) has reassigned to the otherwise Silurian genus *Schlotheimophyllum* some species from the Devonian of the Falls of the Ohio, previously considered to be *Ptychophyllum*. They differ from the latter in having greatly dilated septa in the marginarium. However, the writer considers that study of their internal structure is required (they are apparently known only from externals). They lack the patellate growth form of *Schlotheimophyllum*, and it is not clear whether they have the flat tabulae and amplexoid septa of *Chlamydo-phyllum*, or the rotated septa and domed tabulae of *S. patellatum*, type of *Schlotheimophyllum*.

Range. Upper Lower Devonian of Europe, U.S.S.R.; upper Lower to lower Middle Devonian, Europe and Australia; lower Middle Devonian, U.S.S.R.

Chlamydo-phyllum minus sp. nov.

Plate 67, figs. 1–8

Holotype. SU 14154, locality Ct–18. *Paratypes.* SU 14149, 14151, 14155–7, 14159, 14161, 14163, 14166–71, 18118, 20126.

Diagnosis. Small turbinate to patellate *Chlamydo-phyllum*, commonly with strong rejuvenescence; septa fairly thin in tabularium, not uniting axially; tabularium narrow.

Description. The corallites are solitary, low, turbinate to rather patellate, with broadly conical bases lacking attachment talons; they frequently show repeated strong rejuvenescence. Adults are normally 20–30 mm. in diameter, reducing to as little as 7 mm. during rejuvenescence. The calice is generally saucer-shaped with a sharp rim, and a shallow flat-bottomed axial pit, around which there may be a low reflexed shoulder.

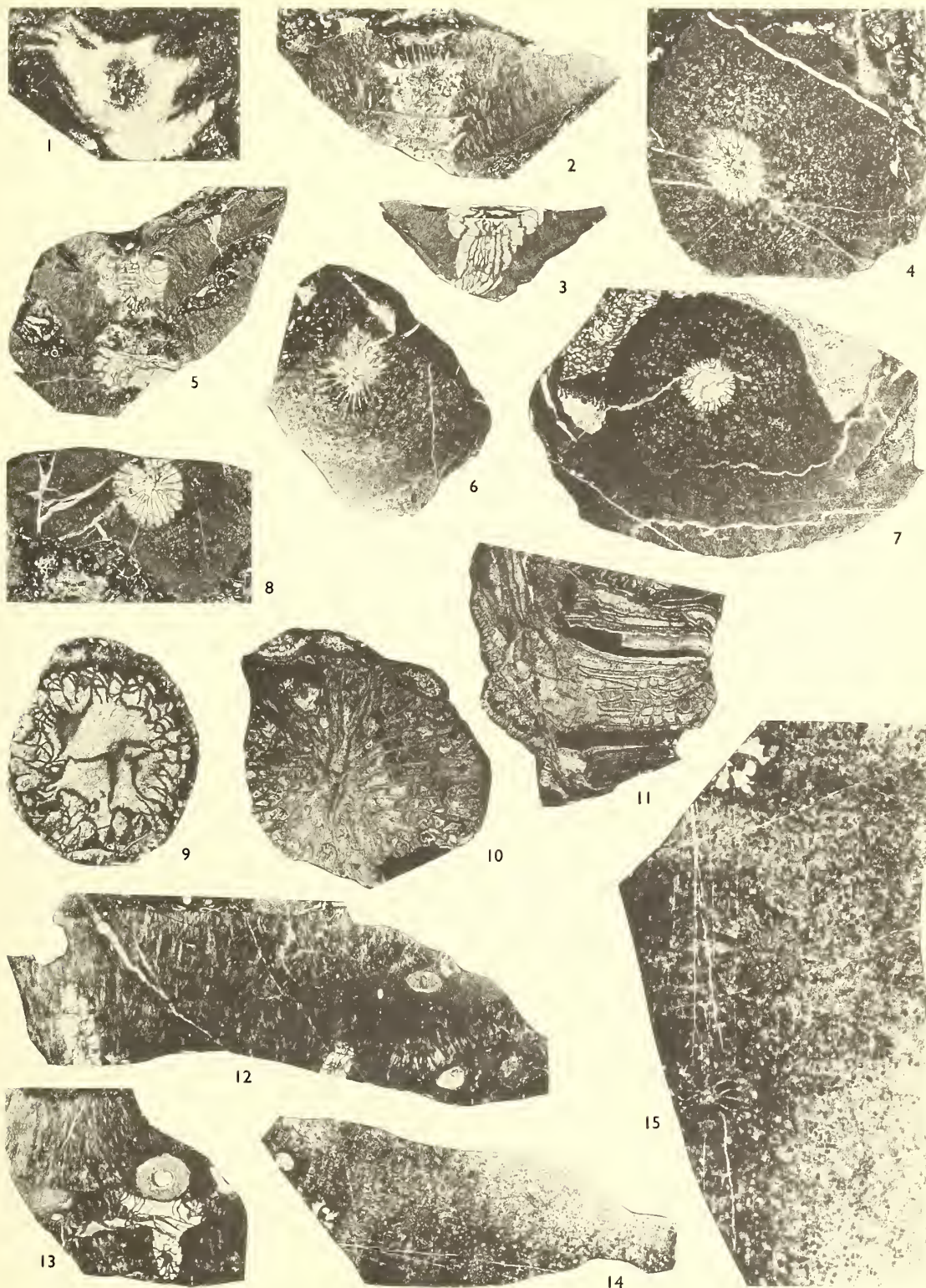
EXPLANATION OF PLATE 67

Magnification $\times 2.0$ unless otherwise stated.

Figs 1–8. *Chlamydo-phyllum minus* sp. nov., loc. Ct–18. 1, holotype SU 14154, viewed parallel to bedding; $\times 1.2$. 2, 5, 6, paratype SU 14171; fig. 2 shows strongly amplexoid septa, and reflexed shoulder around axial pit; fig. 6 shows strongly dilated septa. 3, paratype SU 14167. 4, paratype SU 14159, with axially rotated moderately dilated septa. 7, paratype SU 14169, with septa withdrawn from axis. 8, paratype SU 14166, with attenuate septa.

Figs. 9–11. *Sinospongophyllum abrogatum* Hill 1942. 9, SU 20127, loc. Ct–53; corallite with thin, rather short septa. 10, 11, SU 12128, loc. BN–2; corallite with somewhat dilated septa extending to the axis.

Figs. 12–15. *Iowaphyllum cabonnense* sp. nov., holotype SU 11277, loc. BC–6. Note *Aulopora*? on corallum surface in fig. 12; division of the sectioned tabularium in fig. 14 was apparently caused by intrusion of a crinoid stem fragment; fig. 15 is part of fig. 14 enlarged to $\times 4.0$, with the sediment-filled lumen of one tabularium inked in to emphasize the septal arrangement.



STRUSZ, Rugosa from Devonian of New South Wales

The septa cross the calice as low, faintly granulated rounded ridges. The outer parts of the calical wall are commonly quite thin. The epitheca is known only from thin sections; it is very thin (c. 0.05 mm.), and shows weak irregular growth wrinkles. In most instances, it is longitudinally weakly fluted, the grooves meeting in thin, low interseptal ridges 1.8–2.8 mm. apart.

Dimensions in millimetres.

SU No.	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i> *	<i>n/Dt</i>	<i>L</i> ₁ **
14154***	29.5	5.0	0.17	—	—	—
14159	21+(c. 30?)	4.7	c. 0.16	46	9.8	0.7–0.9 <i>Rt</i>
14166	17.5+	5.5	c. 0.31	48	8.7	0.8–1.0 <i>Rt</i>
14166	c. 23 (worn)	4.2 av.	c. 0.18	44	c. 10.5	0.4–0.9 <i>Rt</i>
14167	18.0+	7.5	c. 0.42	—	—	—
14169	c. 31	4.4	c. 0.14	48	10.9	0.2–0.4 <i>Rt</i>
14171	18.0+	5.0	c. 0.28	50	10.0	0.7–1.0 <i>Rt</i>

* measured at margin of tabularium; ** in tabularium; *** holotype;

Rt = radius of tabularium.

In adults, *n* = 44–50; the septa are dilated to contact both vertically and laterally in a wide marginarium. The minor septa end abruptly at its inner margin, while the major septa extend almost to the axis as thin to moderately dilated, generally slightly curved lamellae, which may be vortically twisted near the axis. The septa are amplexoid, in some cases quite strongly (e.g. SU 14169—see table above), and occasionally bear sparse axial lobes. The septa consist of 0.1–0.2 mm. thick irregular rods of fibrous calcite, directed perpendicularly to the calical surface. Fine recrystallization has in most cases obscured the inner structure of these rods, but some sections suggest that they are probably monacanthine trabeculae. Within the tabularium, the septa consist of a single series of trabeculae, but in the marginarium this may increase to perhaps four or five rather irregular series. In this region, the marginal trabeculae may be directed gently away from the plane of the septum, in which case neighbouring septa are clearly distinguished. In other cases all the trabeculae are more or less vertical, and the individual septa may lose their identity.

The tabulae show some variation. They range from simple, rather distant flat tabulae to flatly domed tabulae with sloping to concave margins. They are usually complete, but in some sections there are additional axial flatly domed tabellae. Particularly where they are fairly simple, the tabulae may be thinly coated with lamellar stereoplasm, partly enveloping the thin to fairly thick amplexoid ends of the major septa.

There are no dissepiments.

Comparison. The only other Australian species, *C. expansum* Hill 1942*b*, is much larger, reaching a diameter of as much as 140 mm. With its liliiform mode of growth, it is intermediate between the European species and *C. minus*. It differs from *C. minus* also in having a relatively wider tabularium, in which the septa are often very strongly dilated, and in having ‘rootlets’ extending from the lower, conical part of the corallite.

The Eurasian species differ from *C. minus* in their conical to cylindrical corallites and relatively wider tabularia.

In its growth form and trabecular structure, this species is very similar to *Schlotheimophyllum patellatum* (Schlotheim 1820)—see Lang (1926, pl. xxx, figs. 4–6). The one

important difference lies in the presence in *C. minus* of strongly amplexoid septa. It is conceivable that *C. minus* is transitional between the two genera.

Remarks. Of the four localities from which this species is recorded, three are biostromal limestones and the fourth is a skeletal calcarenite laterally equivalent to one of the biostromes. The type locality is an outcrop of pink biostromal limestone consisting of coarse crinoidal debris stabilized by broad laminar *Favosites*. The corallites of *C. minus* sat in this coarse sand rather like downward-pointing arrow-heads, clearly unattached but held in place by their shape (as is the larger Recent *Fungites*).

Known localities: Ct-18 (type locality: 20 specimens collected); Ct-28 (same horizon: 7-8 specimens); CAT/2193 (same horizon: 3 specimens); Gn-20 (1 specimen).

Family CHONOPHYLLIDAE

Genus *Iowaphyllum* Stumm 1949

Type species. *Smithia johanni* Hall and Whitfield 1872, p. 234, pl. ix, fig. 10; Upper Devonian, Iowa, U.S.A. Subsequent designation Stumm (1949, p. 50).

Diagnosis. See Stumm (1949, p. 50).

Range. The only previous extra-American record of the genus is *I. cunctum* (Pořta 1902) from the Bohemian Lower Devonian; the new species described below is from the Emsian.

Iowaphyllum cabonnense sp. nov.

Plate 67, figs. 12-15

Holotype. SU 11277, loc. BC-6.

Diagnosis. *Iowaphyllum* with small corallites completely lacking dissepiments; septa few, the major fusing axially to form a columella.

Description. The thamnastraeoid corallum takes the form of mat-like layers superposed one above the other, partly connected and partly separated by sediment; the layers vary in thickness from 3 mm. to over 15 mm. The basal holotheca, which occurs on the under surface of each layer, is moderately wrinkled. The upper surface of each layer is flat, crossed by subdued rounded septal ridges; individual calices are not distinguishable. The calical pits, 2-3 mm. in diameter, are shallow and cylindrical, with rims generally level with the corallum surface, and floors which are flat with a low axial boss. Their centres are 5-15 mm. apart, generally 8-10.

The septa, twenty-two-twenty-six in adult corallites, are dilated to contact throughout the marginarium. The minor septa end abruptly at its inner margin. The major septa continue into the tabularium as thin or moderately dilated, straight or curved lamellae. They unite axially, expanding to form a strong columella. At times they become axially discontinuous, forming amplexoid septal crests on the upper surfaces of the tabulae. In other cases the septal dilatation may spread over the surfaces of some tabulae as thin layers of fibrous calcite.

Dt = 2–3 mm. The tabulae are close, mostly complete, and generally slightly domed with concave margins. They may, however, be flat or sagging, with upturned margins. The columella is reinforced by occasional domed axial tabellae.

There are no dissepiments.

Comparison. In general appearance, and in their dense structure, the closest to *I. cabonnense* sp. nov. are *I. alpenense* (Rominger 1876) and *I. knotti* (Davis 1887). In 'hand specimen' *I. cabonnense* appears as structureless, almost porcellaneous, calcite; its microstructure is only clearly visible in thin section. These two American species appear to be rather similar in appearance, and probably therefore have similar internal structures, lacking dissepiments (see Stumm 1953, cards 102, 105, 106; 1964, p. 48). *I. alpenense*, from the middle Middle Devonian of Michigan, differs from *I. cabonnense* in: (1) having clearly discernible shallow calices separated by low ridges; (2) having more septa ($n = 30\text{--}40$); (3) larger maximum *Dt*. *I. knotti*, from the upper Middle Devonian of Kentucky, the surface of whose corallum is as flat as that of *I. cabonnense*, differs in larger size and more numerous septa ($n = c. 60$).

The remaining American species, all from the Lower Upper Devonian Hackberry Group of Iowa, form a group in which layers of extremely dilated septa are interspersed with layers of large flat dissepiments. All have *Dt* = about 3–5 mm., and n = about 30–40. *I. marginatum* (Fenton and Fenton 1924) has closely spaced calical pits (*Ts* = 8–10 mm.) with large axial bosses and everted rims. *I. johanni* (Hall and Whitfield)—the type species—shows considerable variation in calical spacing (*Ts* = 7–25 mm.), but generally this is noticeably greater than in *I. marginatum*. *I. johanni multiradiatum* (Hall and Whitfield 1872) is stated to have '... larger corallites ... and on the average, more numerous septa ...' than *I. johanni* (see Stumm 1953, card 108), but from the figures given by Stumm this is not immediately apparent. Study from more abundant material of the degree of variability may show that there is in fact no significant difference between the two.

I. cunctum (Počta 1902), from the Lower Devonian Slivenec Limestone of Bohemia (see Prantl 1951, and Chlupáč 1962, p. 15), is closest to the American Upper Devonian group in size, in number of septa, and in having a marginarium containing large flat dissepiments. It differs from all other species of the genus in that the septa frequently remain fairly strongly dilated in the tabularium. The tabulae do not form the flat-topped domes characteristic of the American species. As described by Prantl (1951, p. 11) the septal microstructure is identical to that of *I. cabonnense*.

Known localities. Known only from the type locality, BC–6.

Genus *Sinospongophyllum* Yoh 1937

Type species. *Sinospongophyllum planotabulatum* Yoh 1937, p. 56, pl. vi, figs. 2–5. Lower Givetian, Kwangsi, South China.

Diagnosis. Solitary; dissepimentarium narrow, consisting of a few large lonsdaleoid dissepiments; wide tabulae generally complete, flat, with down-turned edges; septa somewhat withdrawn from the axis. (After Hill 1942*b*, and in Moore 1956).

Range. Known from the Givetian of China and the Emsian? of Australia. The very

similar, probably closely related genus *Tabulophyllum* Fenton and Fenton 1924 is known from the Middle and Upper Devonian of North America, Australia, and Eurasia.

Sinospongophyllum abrogatum Hill 1942

Plate 67, figs. 9–11

1942b *Sinospongophyllum abrogatum* Hill, p. 20, pl. i, figs. 9–11.

Diagnosis. ‘*Sinospongophyllum* with some skeletal dilatation, with marked rejuvenescence, and with tabulae frequently replaced by tabellae’ (Hill 1942b, p. 20).

Remarks. The limited Garra material differs from that of the Mt. Etna Limestone in having shorter major septa, and more generally complete tabulae. However the similarity of over-all structure is such that there can be little doubt of specific identity, even though later study of more abundant material from both localities may show consistent differences at a subspecific level.

Garra localities. BN–2 (1 specimen), Ct–53 (1 specimen), ? Cr–36b (1 specimen?).

Re-evaluation of the Silverwood and Mt. Etna faunas (Queensland)

Hill (1942b) noted the strong similarity of the Mt. Etna and Garra faunas, assigning them both to the Coblenzian. When describing the Silverwood fauna (1940) she assigned it to the Lower Couvinian, but later (1943) considered that it could be older. The writer has since had the opportunity of collecting considerable additional material from the Garra Formation, so greatly expanding the list of species now known from that sequence. He has also been able to examine the collections of corals from the two Queensland limestones held by the University of Queensland. On this basis, and taking into account recent revisions by European workers and the writer (Strusz 1965a, and in press), the accompanying comparative table has been drawn up (Table I).

Examination of Table 1 reinforces the suggestion of similarity between the Garra and Mt. Etna faunas. Of the Mt. Etna corals, about 60 per cent. are also known in the Garra fauna. The only significant difference is that the Mt. Etna fauna is much poorer (at least sixty-five species are now known to the author from the Garra fauna). The Silverwood fauna is less numerous still, but shows considerable similarity to the other two: 40 per cent. of the species occur in the Garra fauna, 30 per cent. in the Mt. Etna fauna.

The writer therefore considers that the three faunas belong to a single association, distinct from both the early Devonian faunas of Victoria (see Philip 1960, 1962; Talent 1963) and the Givetian faunas of Tamworth and North Queensland (Hill 1942c, 1942a). At present, from a consideration of the large Garra fauna, the age would appear to be Emsian, although it may extend into the earliest Eifelian. Finer subdivision, and thence more accurate correlation with the standard European successions, awaits detailed work on the limestones of Taemas (N.S.W.), the Mudgee district of N.S.W. (presently being studied by Dr. A. J. Wright), and the Broken River area of North Queensland (see Hill and Denmead 1960, pp. 149–51; at present being studied by Mr. J. S. Jell). All contain faunas which have at different times been referred to the Lower or lower Middle Devonian.

TABLE 1

	Garra	Mt. Etna	Silverwood
<i>Acanthophyllum</i> (<i>Neostriophyllum</i>) <i>implicatum</i>	x	x	x
<i>Acanthophyllum</i> sp. or <i>Dolmophyllum</i> sp.		e ¹	
<i>Battersbyia</i> sp. cf. <i>conglomeratum</i>			x
<i>Billingsastraea</i> <i>carinata</i>		x	
<i>Calceola</i> sp. ²	x	x	
<i>Chlamydothyllum</i> <i>expansum</i> ³		x	x
<i>Chlamydothyllum</i> <i>minus</i> sp. nov. ³	x		
<i>Hexagonaria</i> <i>densa</i>			x
<i>Hexagonaria</i> <i>lata</i>			x
<i>Plasmophyllum</i> (<i>Plasmophyllum</i>) <i>caespitosum</i> ⁴	x	x	
<i>Plasmophyllum</i> (<i>Plasmophyllum</i>) <i>secundum</i> ⁵	x	x	
<i>Pseudamplexus</i> <i>princeps</i>	x	x	x
<i>Pseudochonophyllum</i> <i>pseudoheliantoides</i>	x		x
<i>Rhizophyllum</i> <i>enorme</i>	x	x	
<i>Radiophyllum</i> <i>arborescens</i> ⁶	e		
<i>Radiophyllum</i> sp. nov. ⁶	x	?	
<i>Sinospongophyllum</i> <i>abrogatum</i>	x	x	
<i>Spongophyllum</i> <i>halysitoides</i> <i>halysitoides</i>	x		
<i>Spongophyllum</i> <i>halysitoides</i> <i>minor</i>			x
<i>Tryplasma</i> sp.		e?	
<i>Xystriphyllum</i> <i>dunstani</i>	x		x
<i>Xystriphyllum</i> <i>insigne</i>		x	

Notes.

¹ e = endemic to that limestone (as presently known).

² Specimens very similar to the small *Calceola* described and figured from the Mt. Etna limestone (Hill, 1942b, p. 15, pl. i, fig. 3) are known from two localities within the Garra Formation.

³ The Australian species of *Chlamydothyllum* are closer to one another than to the Eurasian species (see pp. 4, 7).

⁴ '*Cystiphyllum*' *conjunctum* Hill 1942d is apparently conspecific with this German Middle Devonian phaceloid 'cystimorph'. The species has also been found at Mt. Etna (UQ 14746). See Birenheide (1964, p. 35).

⁵ Birenheide (1964, pp. 23-24) places '*Cystiphyllum*' sp. Hill 1942d, from Wellington, in *Pl. (Plasmophyllum)* *originale* Birenheide 1964, but the writer's collections show that it belongs with the other Australian 'cystimorphs' placed by Birenheide in *Pl. (Pl.)* *secundum*.

⁶ The specimens from Mt. Etna described as *Radiophyllum* *arborescens* are not conspecific with the Garra type. They may be conspecific with a new large species of *Radiophyllum* collected (but not yet described) from the Garra Formation by the writer; alternatively they may belong with *Sterictophyllum* Pedder 1965.

APPENDIX OF LOCALITIES

The general positions of these localities are shown in text-fig. 1; they are shown in somewhat more detail in Strusz (1965a). Detailed maps are contained in Strusz (1963). Grid references, given to the nearest 100 yds., are to the Dubbo (SI 55-4) and Bathurst (SI 55-8) 1:250,000 topographic maps. Further information may be obtained from Strusz (1963, 1965a).

- BC-6: portion 70, Parish Boree Cabonne, Co. Ashburnham; in Mousehole Creek, 1,810 yds. east from the Orange-Parkes highway. Bathurst sheet, grid ref. 1796.8890. 'Rubbly' limestone.
- BN-2: junction of portions 4, 9, and 120, Parish Boree Nyrang, Co. Ashburnham; west bank of Walkers Creek, just west of road bridge. Bathurst sheet, grid ref. 1803.8928. Calcarenite (biostromal?).

- Cr-36b: portion 173, Parish Curra, Co. Gordon, just west of Portion 112, and 150 yds. south of portion 172; near gully, south of the Wellington-Parkes road. Dubbo sheet, grid ref. 1836.9672. Calcarenite.
- Ct-18: portion 45 (NW. sector), Parish Catombal, Co. Gordon, about 100 yds. east of portion 38; in gully (a tributary of Back Creek). Dubbo sheet, grid ref. 1755.9444. Pink biostromal limestone.
- Ct-28: portion 40 (SW. corner), Parish Catombal, about 30 yds. east of junction with portions 30 and 45; field outcrop south of gully, 'Catombal' property. Dubbo sheet, grid ref. 1747.9437. Yellow biostromal limestone (same horizon as Ct-18).
- Ct-53: portion 58 (N. side), Parish Catombal, midway between portions 77 and 79; south bank of Loombah Creek, extending over the interval 75-200 yds. north of the road. Dubbo sheet, grid ref. 1767.9391. Coral-brachiopod biostrome.
- Gn-20: portion 30 (NW. corner), Parish Gundy, Co. Gordon; south side of Wellington-Parkes road, about 900 yds. east of Suntop Public School. Dubbo sheet, grid ref. c. 1795.9699. Calcarenite (biostromal?).
- CAT/2193: 2,193 ft. along measured section CAT from the start point (the east side of the base of a pair of wheat silos, 'Catombal' property); on fence separating portions 41 and 43, Parish Catombal, and 1,160 ft. east from its junction with portion 29. Dubbo sheet, grid ref. 1755.9429. Grey skeletal calcarenite (same horizon as Ct-18, Ct-28).

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ORDOVICIAN CHITINOZOA FROM SHROPSHIRE

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ABSTRACT. Chitinozoan assemblages from the Llanvirnian, Llandeilian, and Caradocian sediments of the Shelve and Caradoc districts of Shropshire have been examined. Thirty-one species belonging to twelve genera are recorded and described; of these, nineteen species and one genus (*Siphonochitina*) are new. The genera *Acanthochitina* and *Hercochitina* are emended. The locations and lithologies of the samples are briefly described and the techniques used in preparing the chitinozoans for microscopic examination are outlined; it has been determined from an examination of material in thin section that these techniques do not appreciably affect the chitinozoans. The character of the chitinozoan fauna in Shropshire is traced from the base of the Llanvirnian to the top of the Caradocian, and the Ordovician faunas of Shropshire, the Baltic, and North Africa are compared. It is concluded that the British fauna, whilst having a distinct character of its own, compares fairly closely with that of the Baltic, but only remotely with that of North Africa. Other acid-resistant microfossils accompanying the chitinozoans are described briefly.

THE Chitinozoa are an extinct group of microscopic marine organisms having hollow organic-walled tests, which are radially symmetrical about a central longitudinal axis and closed at one end. They vary greatly in shape and the test wall may be smooth or furnished with various types of processes. Little is known about the detailed structure of the test, but its original chemical composition, though not certainly known, was probably pseudochitinous (Collinson and Schwalb 1955). Chitinozoan tests may occur singly or they may be joined together in various ways to form chains; rarely, tests are found loosely attached in an organic cocoon (Kozłowski 1963). Single tests are thought to result from the dissociation of members of a chain or the break up of a cocoon. The systematic position of the Chitinozoa is not known, yet they are occasionally referred to the Protozoa. They have certain characteristics in common with the flagellates and others in common with the rhizopods, but they do not fit perfectly into either class of protozoans (Eisenack 1931, 1932; Collinson and Schwalb 1955). Kozłowski (1963) maintains that the Chitinozoa are not protozoans but are remotely analogous with the eggs and egg capsules of existing metazoans. The present consensus of opinion appears to be that these organisms were benthonic; it is my own belief that for part of their lives some forms (e.g. *Cyathochitina kuckersiana* (Eisenack 1934), *Lagenochitina baltica* Eisenack 1931 and *L. shelveensis* sp. nov.) were benthonic and attached to the substrate, and later became free living. The group was already well-established in Arenig times, and flourished during the Ordovician and Silurian; it survived into the late Devonian and is of wide geographical distribution.

Several palaeontologists (Lange 1952, Collinson and Schwalb 1955, Collinson and Scott 1958, Taugourdeau and Jekhowsky 1960, Jodry and Campau 1961) have expressed the belief that this little-known group of microfossils promises to be of considerable value in the correlation of Palaeozoic rocks. Among their reasons for this belief they state that: (1) Chitinozoans have a wide geographical distribution; Taugourdeau and Jekhowsky (1960) claim that in the Sahara, zones based upon chitinozoans persist for over a thousand kilometres. (2) Many species have short vertical ranges. (3) They are virtually indestructible, so they are preserved in great numbers and they can be processed easily, being recoverable from strong acid residues. (4) It has been established

that chitinozoan species in the Devonian of North America have considerable lateral distribution independent of facies changes (Collinson and Scott 1958, p. 5).

Previous work on chitinozoans from Britain is limited to two short publications: Lewis (1940) recorded two species in thin sections of the Upper Caradocian Phosphate Deposits of Montgomeryshire, and Rhodes (1961) described an assemblage from the Nod Glas Formation of Merioneth. The aims of the present paper are to describe assemblages of British Ordovician chitinozoans, to compare them with Ordovician assemblages from the Baltic and North Africa, and to discuss the stratigraphical distribution of forms encountered in the Llanvirnian and Llandeilian sediments of the Shelve area and in the Caradocian sediments of the Caradoc area. Arenig and Caradocian chitinozoans from the Shelve area will be described in a subsequent publication. It is hoped that this work will form the basis for further research on British chitinozoans, particularly within the Welsh Borderland.

To assess the stratigraphical value of these microfossils requires a systematic study of their vertical distribution within a reasonably restricted area, preferably where the age of the rock is known from other fossil evidence. The successions in the Shelve Inlier and the Caradoc area appear to be most suitable for such a study because they are considered to be fairly complete, are exposed within a small area, and have experienced relatively little metamorphism; the geology of both areas has received much attention from palaeontologists and stratigraphers and is sufficiently well understood and documented to provide fairly precisely dated rock samples.

Location of samples. In the Shelve area, samples were collected from exposures described and dated by Whittard (1955); recently, in correspondence, Professor Whittard has been able to precisely date many of them. Samples from the Caradoc area were collected from exposures described and dated by Bancroft (1949), Whittard (Geol. Ass. Guide No. 27), and Dean (1958). Owing to the absence of continuous exposures through most formations, samples were not collected at regular stratigraphical intervals and there is uncertainty, particularly in the Shelve succession, about the precise stratigraphical positions of some samples. However, there is no doubt about the relative positions of the samples, and the correct chronological order of the chitinozoan assemblages obtained from them is known.

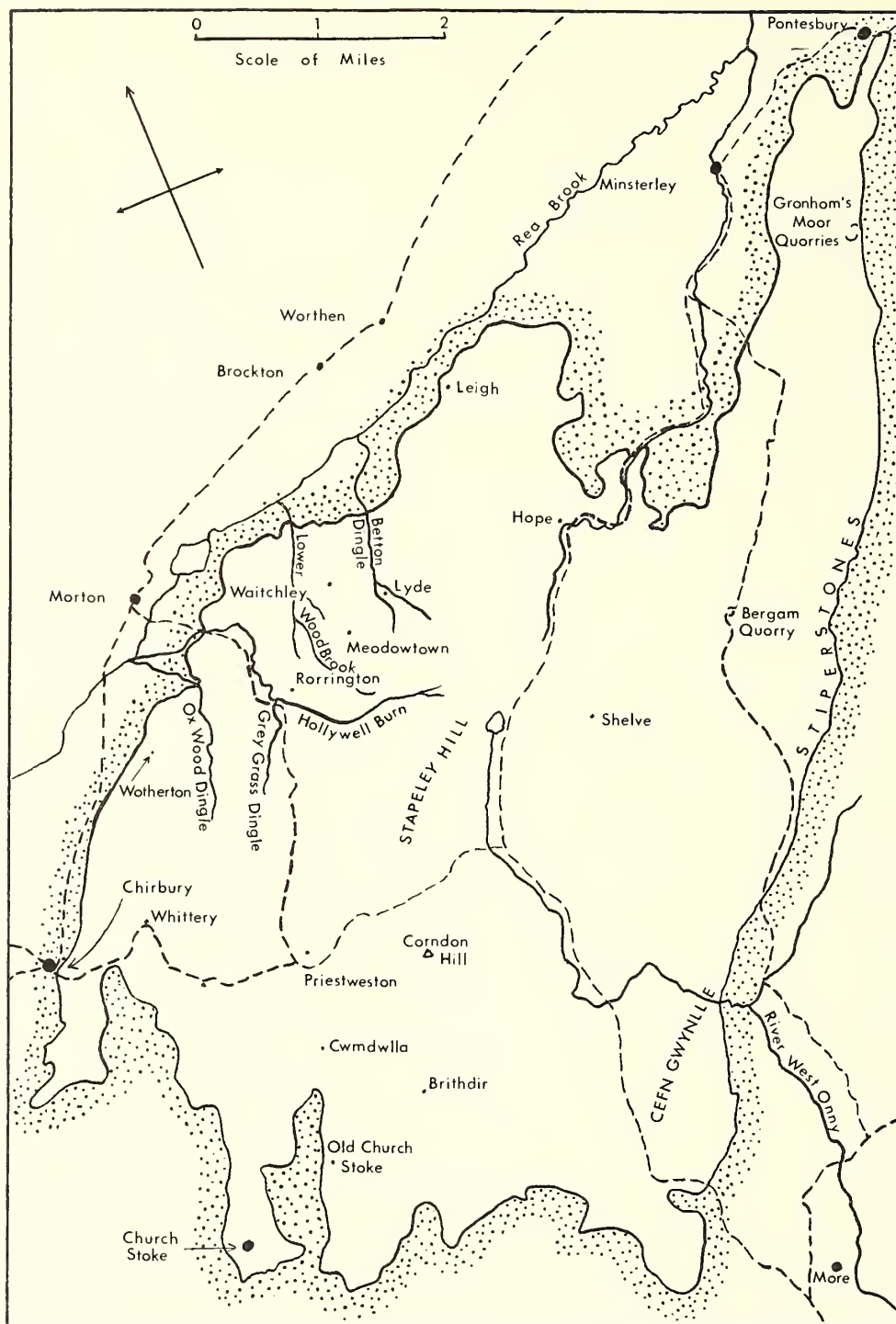
Shelve area. Hope Shales. S25 Massive rusty-weathering black shale from base of Hope Shales, Hope Dingle, behind Hope Cottage and 23 ft. upstream from stone and brick outhouse behind cottage; G.R. 33/345014. S24 As for S25, but stratigraphically higher and 12 ft. further upstream. S21 As for S25, but stratigraphically above S24 and 25 ft. upstream from S25. S22 'Chinastone Ash', half-inch stratigraphically above S21. S23 Olive-green soft shale, half-inch band in 'Chinastone Ash', 6 in. stratigraphically above S21. S26 'Chinastone Ash', 33 ft. upstream from S25 and stratigraphically above S23. S27 'Chinastone Ash', about 40 yd. along road to Lord's Stone from main road through Hope village, in north-east bank of road, 28 in. stratigraphically above lowest horizon in small anticline; G.R. 33/342015. S28 Black shale, 8 in. stratigraphically above S27. S29 Greenish-black shale, near top of Hope Shales, from roadside excavation in Lordstone Lane (Leigh), 230 yd. south-east of Blue Barn; G.R. 33/335025. S36 Blue-black rusty-weathering fissile shale, about 500 ft. stratigraphically below summit of Hope Shales, behind Brithdir Farm, 1 mile east-north-east of Old Church Stoke; G.R. 32/301953.

Stapeley Shales. S37 Yellow-brown crumbly gritty rock from Passage Beds between Stapeley Shales and Weston Beds, collected about 210 yd. south-south-east of Cwmdwla Farm; on lithological grounds Whittard is inclined to include these beds in the Stapeley Shales; G.R. 32/291962.

Weston Beds. S1 Brown weathered micaceous shale, about 200 ft. stratigraphically below top of Weston Beds, in angle between the two streams east of Lyde; G.R. 33/318015.

Betton Beds. S2 Black flags, 200 ft. stratigraphically above base of Betton Beds, in Betton Dingle, about 10 yd. downstream from road, Lyde; G.R. 33/316017.

Meadowtown Beds. S7 Black micaceous hard shale, 12 ft. stratigraphically below S8. S8 Black



TEXT-FIG. 1. Map of the Shelfe area showing the Ordovician outcrop (enclosed by stippling) and some of the places referred to in the descriptions of the sample localities.

micaceous hard shale, about 130 ft. stratigraphically above base of Meadowtown Beds, high horizon in Meadowtown Quarry; G.R. 33/311011. S3 Massive blue-grey limestone, Middle Meadowtown Beds, in lane from Meadowtown to Waitchley, about 140 yd. due north of chapel; G.R. 33/311014. S4 Massive highly calcareous blue-grey rock, Middle Meadowtown Beds, located 22 yd. north of and stratigraphically above S3. S5 Highly calcareous black and brown thinly laminated flagstone, 2 ft. stratigraphically above S4. S6 Decalcified rusty-weathering flagstone, 520 ft. stratigraphically below top of Meadowtown Beds, in small excavation in corner of field, alongside cart-track from Meadowtown to Waitchley; G.R. 33/311015. S11 Dark olive shale, 290 ft. stratigraphically below top of Meadowtown Beds, 12 yd. east of where Rorrington-Meadowtown road crosses Lower Wood Brook, 6 ft. above road in south bank, in small excavation; G.R. 33/307009.

Caradoc area. Coston Beds. C16 Shelly sandy limestone, from lenticular shell-bed containing abundant *Harknessella*, exposed in quarry in New Plantation on north-west side of Lodge Hill, Ruckley; G.R. 32/516994. The Costonian limestones of the north containing *Harknessella* are considered by Dean (1958, p. 200) to be equivalent in age to the *Harknessella* Beds and *Costonia ultima* Beds of the south, the strata containing *Harknessella* being diachronic; the sample is probably Middle or Upper Costonian in age.

Smeathen Wood Beds. C13 Greenish-grey sandy mudstone, 10–25 ft. stratigraphically above base of Harnagian, in old cart track, 60 yd. north of extreme south-east corner of Smeathen Wood, Horderley; G.R. 32/406855.

Glenburrell Beds. C11 Olive-green shaley mudstone with concretions, basal mudstones of Glenburrell Beds, exposed by north side of cartway, north-west of Glenburrell and about 75 ft. north-east of stackyard gate; G.R. 32/412862.

Upper Horderley Sandstone. C10/c Olive-green to yellow-brown, purple-spotted sandstone, 10 ft. stratigraphically below C10/b. C10/a As C10/c, but 6 ft. stratigraphically below C10/b. C10/b Decalcified green shelly sandstone, top Horderley Sandstone, a few feet below Alternata Limestone phase, from highest horizon in quarry by side of New House, Horderley; G.R. 32/417859.

Alternata Limestone. C9 Greenish shelly sandstone, in side of old railway cutting, a few yards south-east of foot bridge over river, south of New House, Horderley; G.R. 32/418857.

Lower Cheney Longville Flags. C8/b Partly decalcified, highly fossiliferous shelly green sandstone, 14 ft. stratigraphically below C8/a. C8/c Laminated green flaggy sandstone, 6 ft. stratigraphically below C8/a. C8/a Slightly calcareous fine green sandstone, from succession of thin-bedded flags, sandy shales, and greenish sandstone; 5 ft. stratigraphically below highest horizon exposed above small pool at north-east corner of Burrell's Coppice, due north of Cheney Longville; G.R. 32/421855.

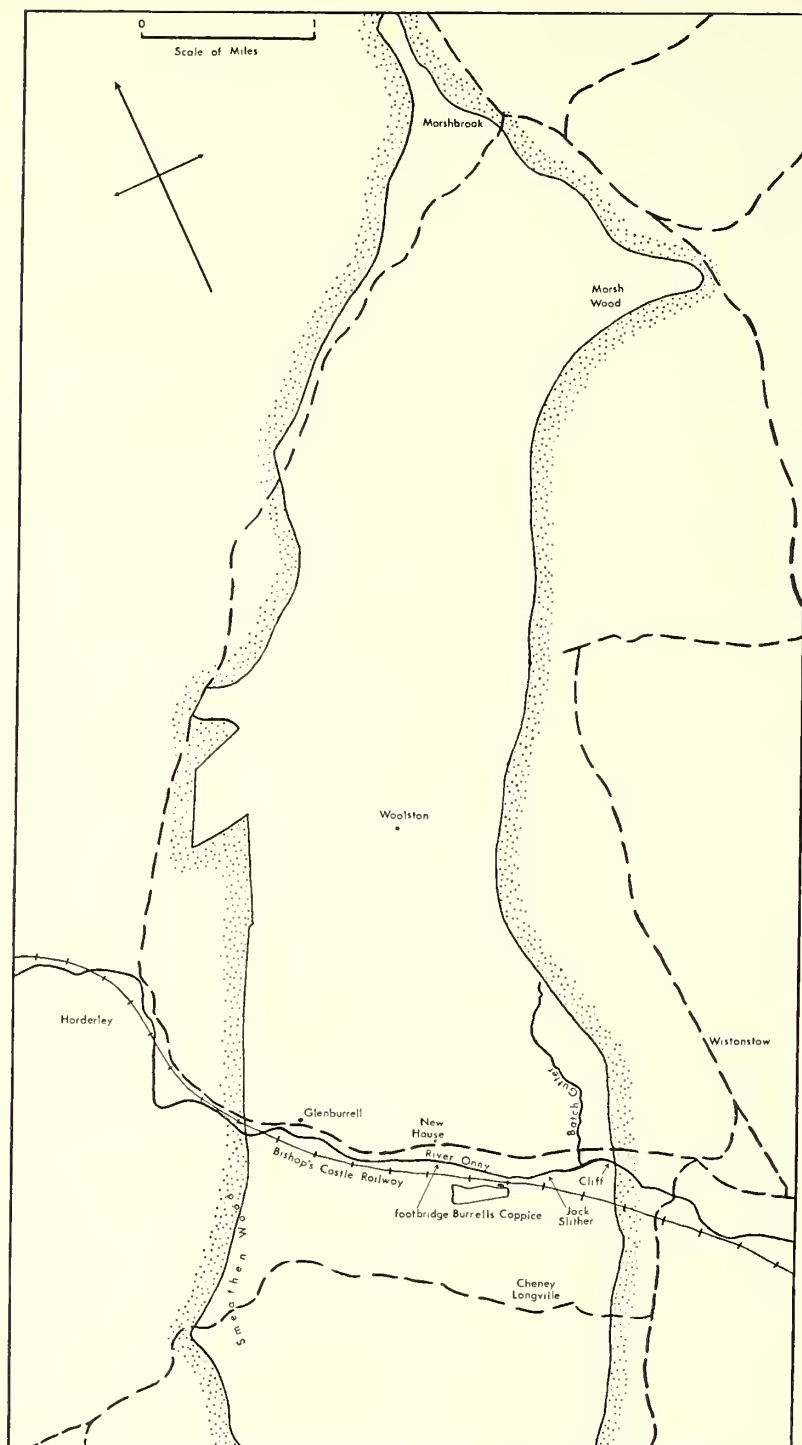
Upper Cheney Longville Flags. C14/b Brownish flaggy siltstone, 18 in. below C14/a. C14/a Highly fossiliferous band within massive olive-green siltstone, Middle Marshbrookian, 7–8 ft. above lowest horizon exposed in Marsh Wood Quarry, about half a mile south of Marshbrook railway station; G.R. 32/443891.

Acton Scott Beds. C6 Olive-green sandy mudstone, basal Actonian, from below tree above Jack Slither, Onny River, Horderley; locality P7, Bancroft 1949; G.R. 32/422854. C4 Highly calcareous grey rubbly micaceous mudstone, containing numerous trilobites, topmost Actonian, from low down in north bank of River Onny, about 85 ft. east of Batch Gutter; locality Py3, Bancroft 1949; G.R. 32/424854.

Onnia Beds. Samples C2/a–d are calcareous blue-grey sandy mudstones. C2/a From low ledge of calcareous mudstone in Onny River about 120 ft. west of 'Cliff Section', Horderley, about 100 ft. stratigraphically above C4; locality Pc, Bancroft 1949; G.R. 32/424854. C2/b 45 ft. downstream from C2/a and stratigraphically 15 ft. higher. C2/c 66 ft. downstream from C2/a and stratigraphically 22 ft. higher. C2/d 110 ft. downstream from C2/a, stratigraphically 38 ft. above C2/a and 15 ft. below C1/a. Samples C1/a–h are orange- to buff-weathering shaley mudstones at top of *Onnia* Beds; they lie 3 ft. (C1/a), 5 ft. (C1/d), 6 ft. (C1/b), 9 ft. (C1/c), 15 ft. (C1/e), 20 ft. (C1/f), 25 ft. (C1/g), and 30 ft. (C1/h) stratigraphically above the lowest horizon exposed in 'Cliff Section', Horderley; G.R. 32/425854.

TECHNIQUES OF PREPARATION AND STUDY

About 250 gm. of sediment were fragmented to about 1 cm. particle size. This size was judged to be the best compromise, smaller fragments yielding more broken chitinozoans, larger ones taking too



TEXT-FIG. 2. Map of part of the Caradoc area showing the Ordovician outcrop (enclosed by stippling) and some of the places referred to in the descriptions of the sample localities.

long to break down in the acid treatment. The fine powder resulting from the fragmentation was discarded since any chitinozoans in it would likely be broken. Dilute hydrochloric acid was used to dissolve the calcareous minerals, 40 per cent. hot (70° C) hydrofluoric acid to disaggregate and remove the clay minerals and quartz; the former was used only if the rock was calcareous. After acid treatment the residue consists mainly of very small particles and the relatively large chitinozoans can be further concentrated by sieving. The sieve (aperture 53 μ) containing the residue was immersed in water to within $\frac{1}{4}$ in. of its top. By gently moving the sieve up and down in the water, keeping the mesh below the water-surface and the top of the sieve above it, the coarser material (including the chitinozoans) was retained while the finer material passed through the mesh into the water beyond. This operation was most successful when a small quantity of the residue was sieved at a time. Several changes of clean water were used, the procedure being continued until no more material passed through the sieve.

Bleaching. During initial experiments to find the most satisfactory method of bleaching chitinozoans, several bleaching agents were used (Schulze's solution, fuming nitric acid, concentrated nitric acid, sodium hypochlorite, and hydrogen peroxide). The experiments indicated that successful bleaching depended not so much on the reagent used but on the state of preservation of the chitinozoans. If the latter were strongly carbonized, as was commonly the case, none of the reagents would bleach them and prolonged treatment served only to break them up; if they were relatively uncarbonized any of the reagents would bleach them. However, sodium hypochlorite is much easier to control than acid reagents, since it can be used under the microscope; its action can be observed and stopped immediately the specimens attain the desired clarity. The most satisfactory method of bleaching the chitinozoans was as follows. A fraction of the residue (roughly a fifth) was transferred in water to a white-bottomed Petri-dish (3.5 in. in diameter, 0.5 in. in depth). When the residue had settled on the floor of the dish the water-level was adjusted to a depth of $\frac{1}{8}$ in. A few drops of sodium hypochlorite solution were then mixed thoroughly into the water and the dish was placed under the microscope. The progress of the reaction was closely observed, and when the chitinozoans were sufficiently translucent the bleaching was stopped by adding an excess of sodium sulphite solution; use of a reducing agent in this manner enables the bleaching process to be precisely controlled even in concentrated solutions of sodium hypochlorite. The residue was then washed by decantation with distilled water until a drop of liquid, taken from the dish after the residue had settled, left no trace of a precipitate when evaporated on a glass slide.

Mounting. The residue, now consisting of chitinozoans, other organic remains, and some insoluble mineral material, was spread thinly over the bottom of a white-bottomed Petri-dish in about $\frac{1}{8}$ in. depth of water and searched systematically under a binocular microscope. Each specimen required for mounting was transferred in a pipette to a second white-bottomed Petri-dish containing distilled water; here, individuals belonging to the same, or apparently similar, species were grouped together and then, in turn, each group was transferred to a watch-glass containing a 2 per cent. aqueous solution of cellosize; only one group occupied this vessel at a time. From here, each specimen was taken up in cellosize solution into a pipette and deposited in a small drop of the solution on a glass coverslip ($2 \times \frac{7}{8}$ in.). Up to thirty such drops, each containing a single specimen, were arranged in rows on each coverslip, which was then placed on a hot-plate (55° C.) for one hour. When dry, each drop of cellosize solution left a thin, tough, colourless transparent film (refractive index 1.50–1.51) adhering to the coverslip; this film holds the specimen against the coverslip and so facilitates its detailed examination at high magnification. The coverslip was then inverted and carefully lowered on to a layer of liquid pre-cooked Canada balsam on a glass slide, which rested on a hot-plate at 120° C.; the balsam had been cooked at this temperature for one to two minutes until it would immediately harden when cooled. These two-layer permanent mounts were immediately ready for filing or use. Ideally, they contained undamaged chitinozoans lying in a single focal plane and quite free of other residual material.

Slide collection. When mounted, each chitinozoan was ringed and given a reference number (e.g. C14/61/1/G) comprising the appropriate sample number (C14), two numbers indicating a particular type of chitinozoan (61/1), and a letter indicating a particular specimen (G). Mounted specimens were examined under a compound microscope in transmitted and oblique reflected light. All the preparations will be housed in the Micropalaeontology Laboratory, Department of Geology, University of Sheffield.

The relative abundance of each species or form was roughly assessed while the microfossils were being picked from the residue. No attempt was made to count the actual numbers of each species or form since generally much of the chitinozoan material consisted of broken, often unidentifiable, fragments. However, it was possible to approximately determine the absolute concentration of chitinozoans and some associated microfossils in two samples (C1/a and S36) where they were exceptionally well-preserved. For both samples, three completely disaggregated residues were prepared by separately digesting three clean fragments (each of known dry-weight) in hydrofluoric acid. The chitinozoans and larger types of associated microfossils in each residue were counted. In C1/a the concentrations were, chitinozoans 156–175 per gm., scolecodonts 5–9 per gm., graptolite siculae 24–39 per gm.; in S36, chitinozoans 32–47 per gm., graptolite siculae 0–2 per gm. Both samples are considered to contain an abundance of chitinozoans and, of all samples examined, C1/a is believed to be among the richest in chitinozoans and graptolite siculae.

Appearance of samples in thin section. Two samples known to contain abundant chitinozoans and other microfossils were examined in thin section; samples C11 and C1/a were chosen for sectioning because of their pale colour, against which the dark chitinozoans stood out clearly. No microfossil material was recognized in sections cut normal to the bedding. In sections cut parallel with the bedding, chitinozoans were seen to lie with their longer axes always in the plane of the section; they and the scolecodonts and graptolite siculae were clearly distinguishable against the pale green, orange, and brownish mineral material. It has been determined from the examination of the specimens in thin section that the techniques used in preparing the microfossils do not (except for bleaching) appreciably alter the chitinozoans.

SYSTEMATIC DESCRIPTIONS

Classification. The straightforward morphological system of classification established by Eisenack is adopted here in preference to the system proposed by Jansonius (1964), which I find difficult to apply to the British material. In the older system chitinozoans are grouped according to their more obvious morphological features, while in the newer system they are, to a considerable extent, grouped into families and genera according to the number of layers in the test wall and the structure of the prosome. In the present material it has generally proved impossible to determine the structure of the test wall, and frequently the prosome is not even discernible. Jansonius's system of classification does not appear to be an improvement on the older system and is considerably less easy to apply. Some of Jansonius's statements, particularly those concerning the structure of the test wall, are not supported by satisfactory explanations or by photographs bearing out his interpretations. Furthermore, it should be noted that the structure of the test wall and the prosome has been interpreted and satisfactorily demonstrated in only a few species.

Terminology. The descriptive terminology proposed by Combaz and Poumot (1962), and by the sub-committee for chitinozoans of the International Committee of the Microflora of the Palaeozoic is adopted in this paper. Until 1955 the terms 'distal' and 'proximal' were applied to the closed and open ends of the test, respectively. Then Collinson and Schwalb (1955) abandoned them, claiming they had been applied in a sense contrary to general usage, and in place of them proposed 'aboral' and 'oral', respectively. The latter terms are used here as proposed by Collinson and Schwalb, while 'distal' and 'proximal' are reintroduced for the restricted purpose of facilitating the description of ornamental and structural processes; these are considered to join the test proximally and to terminate distally. When the neck and siphon are cylindrical their diameters are each expressed in a single measurement. When they are flaring, their

diameters are each expressed by two values, the first (left of the arrow) indicating the diameter closest to the chamber, the second indicating the terminal diameter of the part concerned. In assemblages from Shropshire the relative abundance of a species is expressed in one of the following terms: rare (less than one example per 1,000 chitinozoans), uncommon (1–10 per 1,000), common (10–50 per 1,000), very common (50–100 per 1,000) and abundant (more than 100 per 1,000).

Order CHITINOZOA Eisenack 1931

Genus ACANTHOCHITINA Eisenack 1931 emend.

Type species. *A. barbata* Eisenack 1931, Ordovician, Baltic.

Emended diagnosis. Variable flask-shaped chitinozoans with ornament of uniformly distributed processes standing normal to test wall. At a uniform distance from the test wall each process divides into a number of arms which lie roughly parallel to the test wall. Arms of adjacent processes may unite to form a more or less complete, raised reticulum. Basal margin may bear more strongly developed processes which can be simple or branching. A membrane may unite marginal processes.

Remarks. This genus, based on one individual and a fragment, was erected by Eisenack in 1931. It was not recorded again until Schallreuter (1963) found a single specimen, which he named *A. secunda*, in Middle Ordovician drift material from the island of Hiddensee. Jansonius (1964) reported 'specimens very close to the type species' from the Middle Ordovician of Anticosti Island, Quebec. The genus is abundant in the upper Caradocian of Shropshire. In all known specimens the maximum diameter lies about half-way along the chamber; the base is commonly flat, occasionally slightly concave or slightly convex.

Acanthochitina barbata Eisenack 1931 emend.

Plate 68, figs. 1–9; text-fig. 3

1931 *Acanthochitina barbata* Eisenack, p. 82, pl. 1, figs. 10 (holotype), 11.

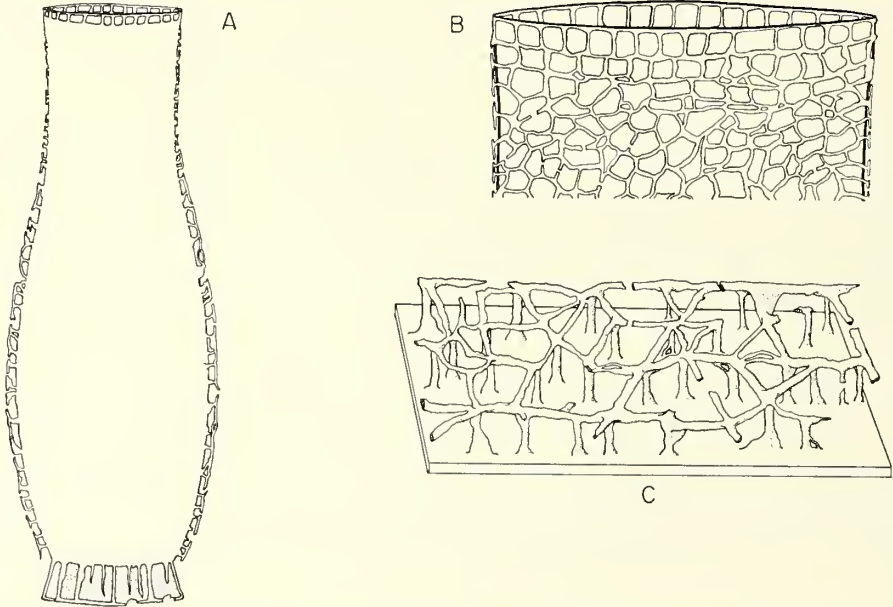
Emended diagnosis. Elongate, swollen cylindrical chamber, generally greater than two-thirds total length; maximum diameter midway along chamber, 35–60 per cent. chamber length; base flat or almost so. Neck cylindrical, about two-thirds maximum diameter in width. Ornament of many closely spaced short processes; arms usually united, forming a fairly complete raised reticulum close to the test wall. Processes on basal margin relatively large, connected by a very thin translucent membrane.

Dimensions in microns. (25 specimens measured.)

	<i>Total length</i>	<i>Maximum diameter</i>	<i>Oral tube diameter</i>	<i>Apertural diameter</i>
Range:	300–485	125–150	75–96	77–107
Mean:	408	134	89	94

Since the chamber and neck often merge gradually, their lengths cannot always be measured precisely

Description. The base appears to be smooth, but in lateral view is usually obscured by the ornament of the basal margin. The collarette is more translucent than the neck and is occasionally slightly flaring. The aperture is straight, but only rarely preserved intact. Processes on the chamber, except those on the basal margin, are very uniform in size (text-fig. 3 A, C) and stand up to $12\ \mu$ in height (about $20\ \mu$ in the holotype). Processes on the oral tube become steadily smaller orally, and, near the aperture, the arms of the



TEXT-FIG. 3. *Acanthochitina barbata* Eisenack 1931 emend. A, Diagrammatic lateral view of test showing ornament only in profile; the membrane connecting the processes on the basal margin is stippled, $\times 190$. B, Detail of oral tube immediately below aperture showing the openings of the reticulum arranged in transverse rows, $\times 550$. C, Reconstruction of the ornament on the chamber wall in full relief, $\times 1,200$.

processes appear contiguous with the test wall. The reticulum is often seen clearly near the aperture (text-fig. 3B), where the test wall is most translucent; immediately below the aperture, the openings of the reticulum are roughly arranged in rows parallel with the transverse axis of the test. Processes on the basal margin are stouter than those

EXPLANATION OF PLATE 68

Figs. 1-9. *Acanthochitina barbata* Eisenack emend. 1, C1/51/2/Z, short example with strongly developed ornament and scarcely distinguishable neck, $\times 190$. 2, C1/51/2/A, typical example, $\times 190$. 3, C1/51/2/F, aboral polar view of isolated base showing strongly developed processes on basal margin, $\times 400$. 4, C1/51/2/B, $\times 190$. 5, C1/51/2/D, $\times 190$. 6, C1/51/2/L, ornamental elements, $\times 625$. 7, C1/51/2/V, ornamental elements, $\times 280$. 8, C1/51/2/J, oral end of oral tube, illustrating the reticulum and the arrangement of the openings roughly into rows parallel with the transverse axis of the test, $\times 370$. 9, C1/51/2/U, aboral end of a specimen having particularly strongly developed ornamental elements, $\times 275$.

Figs. 10-11. *Ancyrochitina onniensis* sp. nov. 10, C1/53/1/C, $\times 400$. 11, C1/53/1/A, holotype, $\times 400$.



JENKINS, Ordovician chitinozoa

elsewhere, and up to $30\ \mu$ in height. The membrane connecting them is always thin, and generally damaged or missing. It may be compared, at least superficially, with the carinae of other forms.

Remarks. Jansonius (1964) reports finding specimens of *Acanthochitina* 'very close to the type species' in Middle Ordovician strata of Anticosti Island. He states that their 'ornaments consist of a mat of intertwined and intergrown spines forming a rough cocoon around the vesicle which constitutes the outer layer of the cuticle'. However, I have been unable to distinguish two wall layers in British specimens of *A. barbata* Eisenack, and am not convinced that the ornament in this species constitutes a distinct structural layer; furthermore, I believe that the term 'cocoon' should be reserved for the sac-like structures described by Kozłowski (1963).

Comparison. Only two species of *Acanthochitina* have been described, *A. barbata* and *A. secunda* Schallreuter 1963. The former was based on a broken specimen and a fragment, the latter on one specimen. I consider that the British specimens belong to *A. barbata* and that the holotype of this species (Eisenack 1931, pl. 1, fig. 10) has lost its oral tube. The only certain difference between the holotype and the British specimens lies in the height of the processes, and this alone is not sufficient, at present, to justify the erection of a new species for the British forms. It is possible that the few very short elevations (1 to $2\ \mu$ high) on the test of *A. secunda* are the remains of an ornament which has been largely lost; many British specimens, having lost much or all of their ornament, closely resemble *A. secunda*. Moreover, it is not uncommon in British examples of *A. barbata* for the processes on the basal margin to be unbranched as they are in *A. secunda* and for the membrane they support to have been lost. Further, if one accepts that the holotype of *A. barbata* has lost its oral tube, then the position of the maximum diameter in *A. barbata* and *A. secunda* is roughly the same and cannot be used to distinguish the two species.

The ornament of *Stephanochitina africana* Grignani and Mantovani 1964 resembles that of *Acanthochitina barbata* in so far as the processes are distributed uniformly, and adjacent processes, discrete for most of their lengths, are joined at their distal ends to form a raised reticulum ('treillis' of Grignani and Mantovani); in other respects the two species are distinct.

Material. Three thousand to four thousand single tests.

Occurrence. *Omnia* Beds: C2/d (very common), C1/a-h (abundant). The type material is from the Lyckholm Beds, F₁, of the Baltic.

Genus ANCYROCHITINA Eisenack 1955a

Type species. *A. ancyrea* (Eisenack 1931), Silurian, Baltic.

Ancyrochitina omniensis sp. nov.

Plate 68, figs. 10-11; Plate 69, figs. 1-2; text-fig. 4

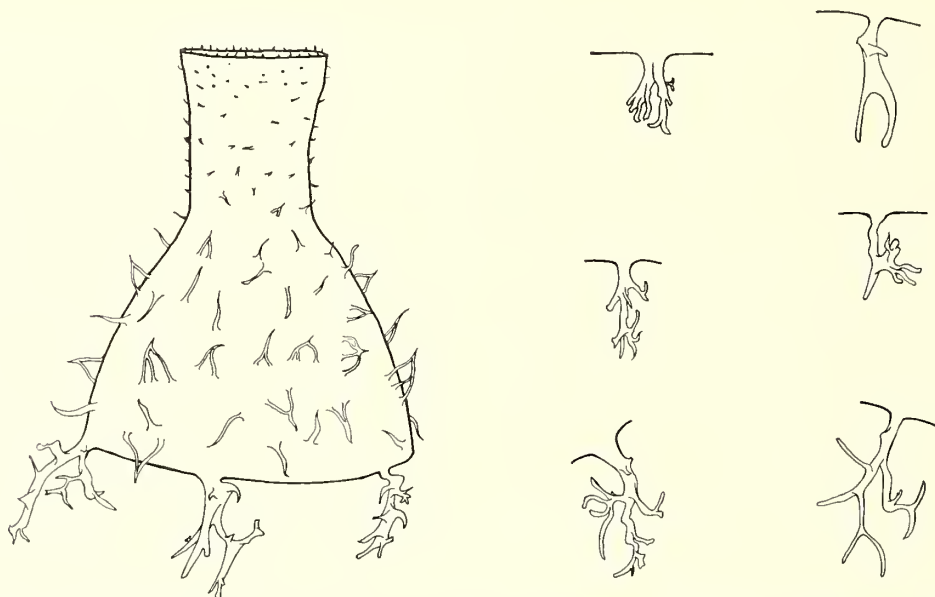
Holotype. Plate 68, fig. 11. Specimen C1/53/1/A; *Omnia* Beds, sample C1/a.

Diagnosis. Small cylindroconical test. Chamber half to two-thirds total length; maximum diameter considerably greater than chamber length; base flat or slightly convex.

Commonly three to six stout branching appendices, about half maximum diameter in length; one to three (rarely four) orders of branching into two to five generally unequal limbs. Neck diameter about half maximum diameter; collarette flaring, with fringe of fine terminal hairs. Small simple spines and wishbone spines thinly distributed over test, absent on base and basal margin.

Dimensions in microns. (25 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Appendix length
Holotype:	108	58	64	50	27 → 38	up to 30
Range:	77–115	46–62	62–75	31–50	24–33 → 38–45	up to 35
Mean:	92	54	68	38	29 → 32	—



TEXT-FIG. 4. *Ancyrochitina omiensis* sp. nov. Lateral view of test (left) and six drawings illustrating variation in the shape and branching pattern of the appendices, $\times 620$.

Description. The flanks of the short broad chamber either taper uniformly or are somewhat swollen and associated with a more or less pronounced shoulder. The maximum diameter is 110–160 per cent. of the chamber length. The appendices appear to be hollow or filled with a granular substance and, where they branch, their courses often alter sharply. Complete appendices are generally 20–30 μ in length. The neck and chamber are distinct and the apical angle is at least 60°. Generally the neck is cylindrical, occasionally flaring, but never tapering. The proportion of simple to wishbone spines is variable but in most specimens the majority are simple. Their distribution on the neck is slightly less dense than on the chamber. Both types of spine measure up to 11 μ in length. Spines which have a single proximal base and multiple distal extremities are unknown in *A. omiensis* sp. nov.

Comparison. Several similar species from the Siluro-Devonian of North Africa differ from *A. omniensis* as follows. *A. tomentosa* Taugourdeau and Jekhowsky 1960 lacks wishbone spines, the ornament being of strong flexible spines, sometimes with multiple distal extremities. In *A. pilosa* Taugourdeau and Jekhowsky 1960 the appendices are simple, or forked only near their distal ends, and the upper part of the neck is strongly ornamented. *A. tumida* Taugourdeau and Jekhowsky 1960 has a very short neck, and *A. multiramosa* Taugourdeau and Jekhowsky 1960 and *A. saharica* Taugourdeau 1962 have between twelve and twenty appendices.

Material. Approximately six hundred single tests.

Occurrence. *Omnia* Beds: C2/b (common), C2/c (abundant), C2/d (very common), and C1/a–h (abundant).

Ancyrochitina alaticornis sp. nov.

Plate 69, figs. 3–13; text-fig. 5

Holotype. Plate 69, fig. 3. Specimen C9/61/1/A; Alternata Limestone, sample C9.

Diagnosis. Elongate bell-shaped chamber, slightly more than half total length; maximum diameter at base, about two-thirds chamber length; base flat, margin sharply rounded. Three to eight curved wing- or blade-like appendices (flattened vertically), up to 60 per cent. maximum diameter in length; aboral edge of appendix thick, entire; oral edge attenuated, irregular in outline, differentiated into secondary processes of variable shape, size, and disposition. Neck cylindrical or slightly flaring, about half maximum diameter in width. Collar short, strongly flaring, with fringe of fine terminal hairs. Wall generally smooth; rarely with minute processes on neck.

Dimensions in microns. (35 specimens measured.)

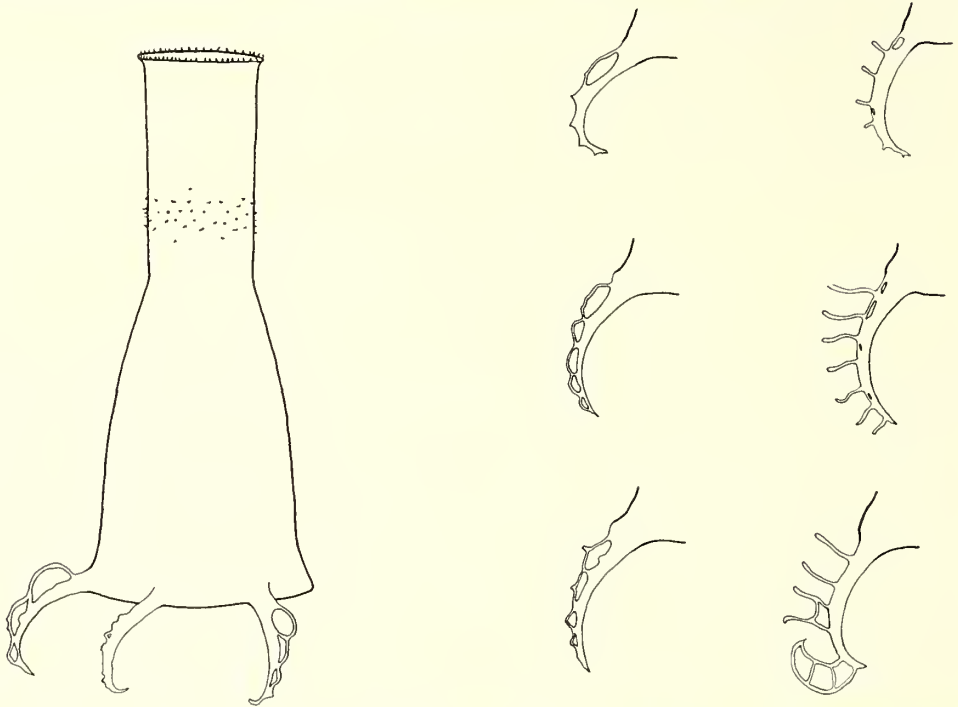
	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Neck diameter</i>	<i>Apertural diameter</i>	<i>Appendix length</i>
Holotype:	171	90	67	81	35	44	up to 34
Range:	123–267	85–165	55–104	—	31–55 → 35–55	40–58	up to 53
Mean:	192	113	80	84	38 → 41	46	—

Description. The roughly conical chamber often narrows rather more rapidly near the base than elsewhere; a swelling is superimposed on the flanks and a slight but distinct shoulder may be developed. The maximum diameter is 60–80 per cent. of the chamber length. Proximally, the appendices are directed laterally outward from the basal margin; distally, owing to their curvature, they come to lie roughly parallel with the longitudinal axis of the test. The thick edge is invariably directed aborally; from it the appendix becomes thinner towards the oral edge. Large and small openings, elongate along the length of the appendix, often perforate the appendices. Occasionally an appendix divides in a transverse plane, joining the basal margin at two or more points (Pl. 69, fig. 7); appendices do not divide to form multiple distal extremities. Generally the test wall is smooth, but in each of four populations from fairly wide stratigraphical intervals (samples C9, C8/b–c, C6) the necks of a few tests bear cones or spines, up to $1.5\ \mu$ in length.

Remarks. The style of the appendices and the shape of the test make *A. alaticornis* sp. nov. quite distinct.

Material. Between four hundred and five hundred single tests.

Occurrence. Alternata Limestone: C9 (abundant). Cheney Longville Flags: C8/b-c (abundant), C14/b (abundant). Acton Scott Beds: C6 (abundant).



TEXT-FIG. 5. *Ancyrochitina alaticornis* sp. nov. Lateral view of test (left) and six drawings illustrating the variation shown by the appendices, $\times 375$.

Ancyrochitina bulmani (Jansonius 1964) comb. nov.

Text-fig. 6

1964 *Conochitina bulmani* Jansonius, p. 907, pl. 1, figs. 3, 4 (holotype).

EXPLANATION OF PLATE 69

Figs. 1–2. *Ancyrochitina onniensis* sp. nov. 1, C1/53/1/R, $\times 400$. 2, C1/53/1/B, $\times 400$.

Figs. 3–13. *Ancyrochitina alaticornis* sp. nov. 3, C9/61/1/A, holotype, $\times 300$. 4, C9/61/1/B, $\times 300$.

5, C6/61/1/K, oblique lateral view of aboral end of test showing arrangement of appendices, $\times 300$.

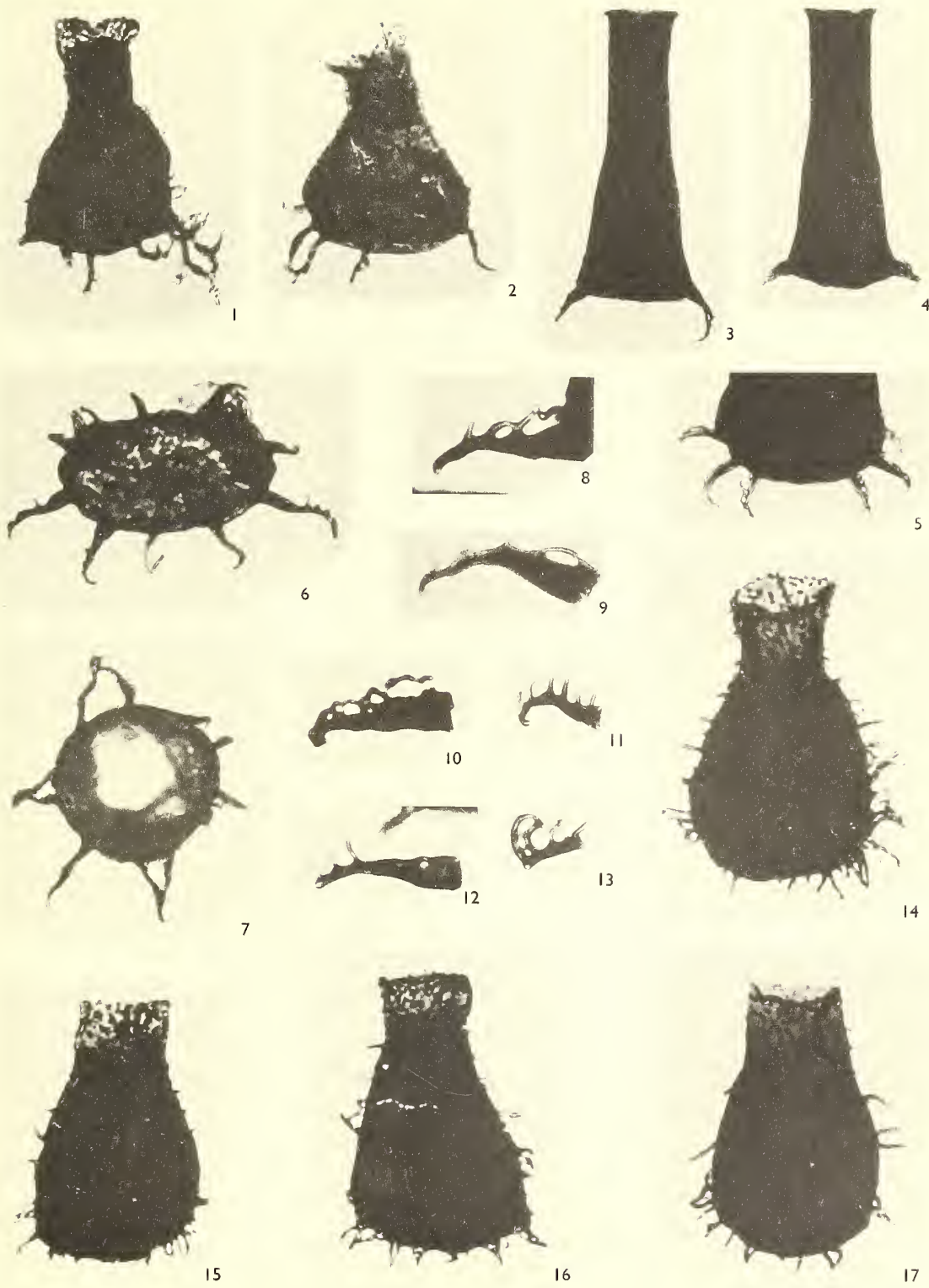
6, C6/61/1/X, oblique aboral polar view of isolated base showing arrangement of appendices, $\times 415$.

7, C6/61/1/Z, polar view of isolated base showing three appendices each joining the basal margin at two points, $\times 275$.

8–13, isolated appendices; showing some of the morphological variation assumed by the appendices. 8, C6/61/1/D, $\times 830$. 9, C6/61/1/H, $\times 625$. 10, C6/61/1/I, $\times 625$. 11, C6/61/1/J, $\times 625$. 12–13, C6/61/1/D, $\times 830$.

Figs. 14–17. *Angochitina communis* sp. nov. 14, C1/54/1/A, holotype, $\times 360$. 15, C1/54/1/C, $\times 360$.

16, C1/54/1/B, $\times 360$. 17, C1/54/1/D, $\times 360$.

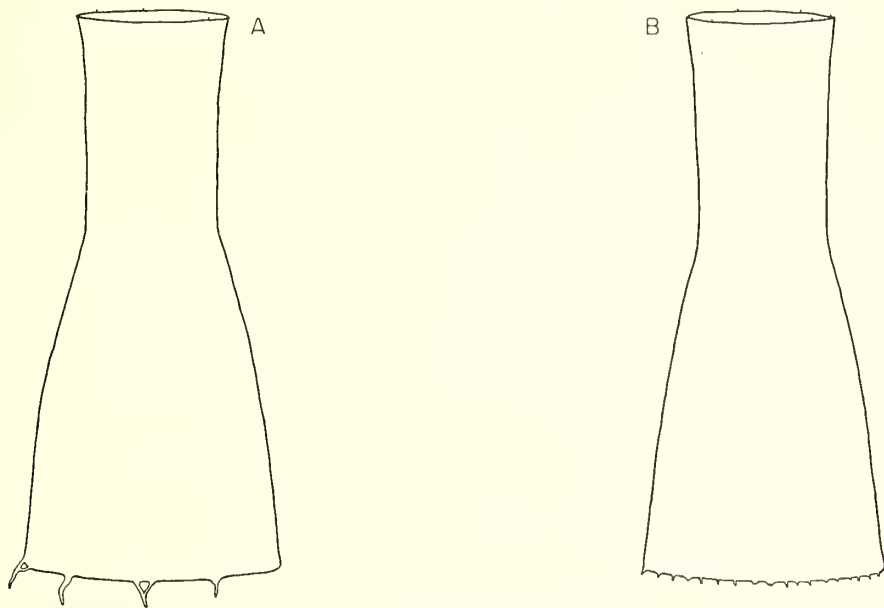


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Dimensions in microns. (18 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Appendix length
Range:	154-180	95-131	69-88	43-80	35-46 → 44-48	up to 11
Mean:	166	101	79	66	41 → 45	—

Remarks. In Shropshire, several specimens identical with that figured by Jansonius (1964, pl. 1, fig. 3) were found in association with otherwise similar forms having smaller and more numerous processes restricted to the narrow, sharply rounded basal margin. These forms, which are similar in age to the Scottish type material, conform closely with Jansonius's description (p. 907) of *Conochitina bulmani*. However, I do not follow



TEXT-FIG. 6. *Ancyrochitina bulmani* (Jansonius) comb. nov. Two extreme forms: A, characterized by a small number of relatively well-developed appendices, and B, characterized by more numerous, but smaller appendices, $\times 450$.

Jansonius's emendation of *Conochitina*, and, by virtue of its well-developed and distinct neck and because the processes are restricted to the basal margin and not merely 'particularly well developed aborally' (Eisenack 1955b), this species is unquestionably closer to *Ancyrochitina* than *Conochitina* emend. Eisenack 1955.

Comparison. *Sphaerochitina collinsoni* Dunn 1959 (Devonian of Iowa) is distinguished from *Ancyrochitina bulmani* by its fungiform test and much longer neck. The processes of *Sphaerochitina nodulosa* Collinson and Scott 1958 (Devonian of Illinois), although somewhat similar to those of *A. bulmani* and confined to the aboral end of the test, are not restricted to the basal margin.

Material. One hundred and thirty single tests.

Occurrence. Glenburrell Beds: C11 (abundant).

Genus ANGOCHITINA Eisenack 1931

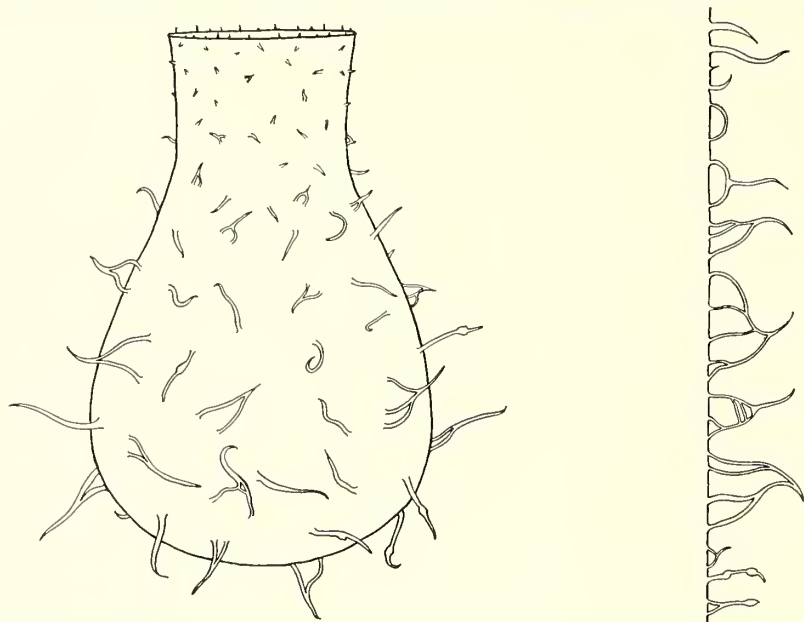
Type species. *A. echinata* Eisenack 1931, Silurian, Baltic.

Angochitina communis sp. nov.

Plate 69, figs. 14–17; text-fig. 7

Holotype. Plate 69, fig. 14. Specimen C1/54/1/A; *Onnia* Beds, sample C1/a.

Diagnosis. Test small. Chamber ovoid, about four-fifths total length; maximum diameter in lower half of chamber, about four-fifths chamber length; base slightly to strongly



TEXT-FIG. 7. *Angochitina communis* sp. nov. Lateral view of test (left) and diagram illustrating the range of variation in shape and complexity of the spines, $\times 575$.

convex. Neck distinct, short, cylindrical, or slightly flaring, about half maximum diameter in width. Collarette with fringe of short hairs. Slender simple and wishbone spines with pointed tips, up to 35 per cent. maximum diameter in length, evenly distributed over whole test.

Dimensions in microns. (25 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Process length
Holotype:	130	92	80	38	39 $\rightarrow$ 46	up to 25
Range:	100–145	75–110	70–85	22–40	35–42 $\rightarrow$ 39–46	up to 25
Mean:	122	90	77	32	38 $\rightarrow$ 42	—

Description. A dark lenticular shape running transversely across the test is often seen near the base; it appears to be a fold in the test wall; no opisthosome has been recognized. The terminal hairs around the aperture are simple and up to $2\ \mu$ in length.

Generally the test bears both wishbone and simple spines, the latter usually predominating. Both types of spine are similar in length, thickness, and texture; they stand normal to the test wall, which they meet abruptly. They are most strongly developed aborally, shortest on the neck. Small node-like thickenings sometimes occur on them and, occasionally, small cross-bars join two limbs of a wishbone spine. The internal surface of the oral tube often bears short simple spines with sharp tips.

Comparison. Several species, including *A. globosa* Collinson and Scott 1958 and *A. milanensis* Collinson and Scott 1958, are similar in shape to *A. communis* but have very different ornamentation.

Material. Six thousand to seven thousand single tests.

Occurrence. *Onnia* Beds: C1/a-h (abundant).

Angochitina dicranum sp. nov.

Plate 70, fig. 1; text-fig. 8

Holotype. Plate 70, fig. 1. Specimen C2/c/54/3/A; *Onnia* Beds, sample C2/c.

Diagnosis. Test small. Chamber ovoid, about two-thirds total length; maximum diameter one-third to half-way up chamber, about three-quarters chamber length; base convex. Neck distinct, slender, cylindrical, about half maximum diameter in width; collarette flaring, with fringe of short terminal hairs. Ornament of sharply pointed, simple, and pitchfork-shaped spines up to half maximum diameter in length, distributed over whole test.

Dimensions in microns. (12 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Apertural diameter	Spine length
Holotype:	147	89	62	58	27	35	up to 23
Range:	101-158	60-120	55-82	33-55	25-38	30-38	up to 30
Mean:	130	86	60	45	32	35	—

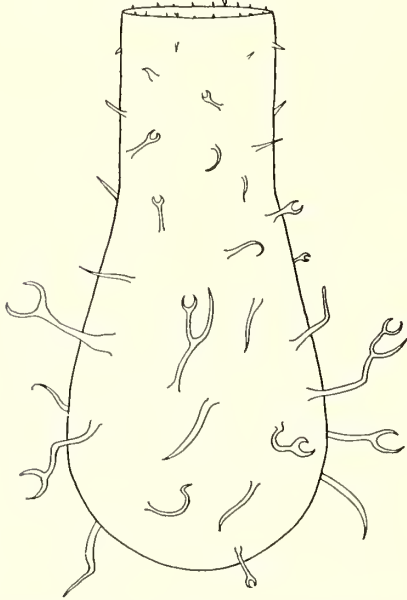
Description. The ornament consists of relatively few spines (10-35 per test), all having pointed tips and standing normal to the test wall, which they meet abruptly. Forked spines have very wide angled bifurcations and are shaped like pitchforks; initially the limbs of each fork diverge rapidly, distally they run parallel with each other but rarely converge. Commonly, forked spines have only first order branching; second order branching is rare. The proportion of simple to forked spines is variable and either may predominate. Both types are roughly the same in length, becoming shorter orally, and are distributed fairly uniformly over the whole test. Near the aperture the inner surface of the oral tube often bears short simple spines with pointed tips. Rarely, the terminal fringe of hairs on the collarette includes small pitchfork-shaped spines.

Comparison. *A. dicranum* sp. nov. and *A. communis* sp. nov. are distinguished mainly by their different ornaments. They are closely similar in size and shape, but the oral tube of *A. dicranum* is slightly longer and thinner than that of *A. communis*. No specimen of *Angochitina* bearing both wishbone spines and pitchfork-shaped spines

was found in Shropshire. In *A. bifurcata* Collinson and Schwalb 1955 all the spines fork, but none is shaped like a pitchfork. *A. capillata* Eisenack 1937 has numerous simple, very short spines.

Material. One hundred and fifty single tests.

Occurrence. *Onnia* Beds: C2/c (very common), C2/d (abundant).



TEXT-FIG. 8. *Angochitina dicranum* sp. nov.
Lateral view of test, $\times 565$.

Genus CONOCHITINA Eisenack 1931 emend. 1955b

Type species. *C. claviformis* Eisenack 1931, Baltic drift.

Original diagnosis (Eisenack 1931, p. 83). 'Chitinozoa with generally conical tests, the maximum diameter lying near the base.'

Upon the establishment of the genera *Sphaerochitina* Eisenack 1955a, *Ancyrochitina* Eisenack 1955a, and *Cyathochitina* Eisenack 1955b, to which were transferred several species from *Conochitina*, Eisenack (1955b) gave the following emended diagnosis for *Conochitina*: 'Chitinozoa with conical tests and rounded basal margins. Wall smooth or bearing numerous more or less short spines, which in general are particularly well developed aborally.'

Conochitina lepida sp. nov.

Plate 70, figs. 2-3

Holotype. Plate 70, fig. 2. Specimen C1/52/1/A; *Onnia* Beds, sample C1/a.

Diagnosis. Wide conical chamber with swollen flanks, about three-quarters total length; maximum diameter at base, approximately equal to chamber length; base almost flat, margin sharply rounded. Neck distinct, cylindrical, half to two-thirds maximum diameter in width. Aperture straight. Wall smooth.

EXPLANATION OF PLATE 70

Fig. 1. *Angochitina dicranum* sp. nov., C2/c/54/3/A, holotype, $\times 415$.

Figs. 2-3. *Conochitina lepida* sp. nov. 2, C1/52/1/A, holotype, $\times 230$. 3, C1/52/1/B, $\times 230$.

Figs. 4-8. *Conochitina chydrea* sp. nov. 4, S21/35/3/A, holotype, $\times 230$. 5, S21/35/8/var. A/2, test not differentiated into chamber and neck, $\times 230$. 6, S21/33/1/C, example with hemispherical base, $\times 230$. 7, S21/35/5/A, $\times 230$. 8, S21/35/9/B, $\times 230$.

Figs. 9-14. *Conochitina parviventris* sp. nov. 9, S36/3/1/J, small example, $\times 230$. 10, S36/3/1/C, $\times 230$. 11, S36/3/1/B, $\times 230$. 12, S36/3/1/H, $\times 230$. 13, S36/3/1/A, holotype, $\times 230$. 14, S36/3/1/E, $\times 230$. The dark transverse bands in the upper parts of some tests (figs. 10 and 12) are discussed briefly in the text.



JENKINS, Ordovician chitinozoa

Dimensions in microns.

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Neck diameter</i>
Holotype:	167	123	108	44	55
Specimen C1/52/1/B:	159	120	102	39	55
Specimen C11/52/1/A:	142+	96	112	46+	69

Description. In the lower half of the chamber the flanks are roughly parallel. They meet the base abruptly, but the basal margin is clearly rounded and there is no evidence of an incipient carina. The base is slightly concave near the margin, becoming slightly convex towards the centre; originally, however, it may have been flat.

Comparison. The swollen flanks and the sharply rounded basal margin distinguish this species from *Conochitina lagenomorpha* Eisenack 1931, *C. filifera* Eisenack 1931, *C. conulus* Eisenack 1955b, and *C. communis* Taugourdeau 1961.

Material. Twelve single tests, the majority of which are damaged.

Occurrence. Glenburrell Beds: C11 (rare). *Omnia* Beds: C2/d and C1/a-c (rare).

Conochitina chlydaea sp. nov.

Plate 70, figs. 4-8

Holotype. Plate 70, fig. 4. Specimen S21/35/3/A; lower Hope Shales, sample S21.

Diagnosis. Test conical or cylindroconical with flat or slightly convex base and rounded basal margin. Maximum diameter at base, 30-40 per cent. total length. Neck cylindrical or slightly flaring, shorter than chamber, about two-thirds maximum diameter in width, not always developed. Aperture straight. Wall smooth or bearing small cones.

Dimensions in microns. (45 specimens measured.)

	<i>Total length</i>	<i>Maximum diameter</i>	<i>Oral tube diameter</i>	<i>Apertural diameter</i>
Holotype:	204	75	52	54
Range:	123-323	57-96	41-71	31-78
Mean:	199	76	55	52

Description. The tests vary considerably in shape. The chamber may be slender or stout, and the neck absent or up to nearly half the total length. Most populations consist of smooth and ornamented individuals, the latter generally forming one-tenth to one-fifth of the population. In the lower and upper Hope Shales the populations consist entirely of smooth specimens, while in a sample from the upper Llandeilian (S11) more than three-quarters of the population are ornamented with small cones up to $1.5\ \mu$ in length. However, it has not been established that there was a trend towards ornamentation. The cones are largest and most densely concentrated at the basal margin; orally they always become smaller and scarcer, and only rarely do they occur on the neck.

Comparison. Several species closely resemble *C. chydaea*; they are *Conochitina simplex* Eisenack 1931, *C. primitiva* Eisenack 1939, *C. intermedia* Eisenack 1955a, and *C. edjelensis* Taugourdeau 1963. They differ from *C. chydaea* as follows. Populations of *C. simplex* contain a few individuals whose bases extend aborally in inverted cones. In *C. primitiva* the flanks taper more rapidly near the base than elsewhere. *C. intermedia* has a simple conical test (no neck) and a larger apical angle. *C. edjelensis* shows similar variation in form to the new species but has a concave base.

Material. Several thousand single tests.

Occurrence. Hope Shales: S25 (abundant), S21 (abundant), S36 (abundant). Stapeley Shales: S37 (abundant). Weston Beds: S1 (abundant). Betton Beds: S2 (abundant). Meadowtown Beds: S8 (abundant), S3 (abundant), S4 (abundant), S5 (abundant), S11 (abundant). Coston Beds: C16 (uncommon). Glenburrell Beds: C11 (uncommon). Onnia Beds: C1/a-h (uncommon).

Conochitina parviventer sp. nov.

Plate 70, figs. 9-14

Holotype. Plate 70, fig. 13. Specimen S36/3/1/A; upper Hope Shales, sample S36.

Diagnosis. Small uniformly tapering conical chamber, 20-30 per cent. total length; maximum diameter at base, 15-20 per cent. total length; base flat or slightly convex, basal margin sharply rounded. Oral tube long, cylindrical, about two-thirds maximum diameter in width; aperture straight. Wall smooth.

Dimensions in microns. (26 specimens measured.)

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>
Holotype:	498	125	85	375	58
Range:	215-498	69-150	58-90	142-375	42-65
Mean:	390	106	74	284	51

Description. *C. parviventer* sp. nov. shows very little morphological variation. The chamber and neck are characteristically distinct, yet their junction is rarely very abrupt. The wall of the oral tube is translucent for most of its length, particularly so near the aperture, becoming progressively more opaque towards the chamber. A collarette cannot be distinguished. Narrow, dark transverse striations frequently cross the oral tube; it has not been determined whether these are elements of an extended prosome or structures within the test wall.

Comparison. The separation of its test into a chamber and oral tube distinguishes *C. parviventer* sp. nov. from *C. elegans* Eisenack 1931. Many examples of both these species have been found in the Welsh Borderland but transitional forms are unknown and the two species were not found together; their known stratigraphical ranges do not overlap.

Material. Seventy-five single tests.

Occurrence. Hope Shales: S21 (rare), S36 (abundant). Meadowtown Beds: S3 (rare).

Conochitina elegans Eisenack 1931

Plate 71, figs. 1–4

- 1931 *Conochitina elegans* Eisenack, p. 87, pl. 2, fig. 4 (holotype).
 1934 *Rhabdochitina conocephala* Eisenack, p. 61, pl. 4, figs. 10–12; text-fig. 32.
 1959a *Conochitina elegans* Eisenack; Eisenack, p. 3, pl. 2, figs. 4 (neotype), 5; text-fig. 1.
 1960 *Rhabdochitina conocephala* Eisenack; Taugourdeau and Jekhowsky, p. 1230, pl. 9, fig. 131.
 non 1962 *Conochitina elegans* Eisenack; Beju and Danet, p. 531, pl. 1, figs. 31, 32.
 non 1964 *Rhabdochitina conocephala* Eisenack; Cramer, p. 351, pl. 22, fig. 14; pl. 23, figs. 7, 11, 12.

Dimensions in microns. (30 specimens measured.)

	<i>Total length</i>	<i>Maximum diameter</i>
Range:	200–616	58–92
Mean:	388	73
26 specimens from Estonia (Eisenack 1959a)	Range: 288–667 Mean: 467	
	Neotype: 482	76

Remarks. A study of much material led Eisenack (1959a) to unite *Conochitina elegans* Eisenack 1931 and *Rhabdochitina conocephala* Eisenack 1934 as one species. The British material leads me also to conclude that the two are the same. Eisenack (1959a, p. 4) remarked that *Rhabdochitina pistillifrons* Eisenack 1939 was possibly an extreme form of *C. elegans*, but he was not able to determine the nature of their relationship owing to the lack of enough specimens. The morphological variation shown by the very numerous British specimens of *C. elegans*, however, does not suggest that *R. pistillifrons* and *C. elegans* are one species.

Except for slight differences in size the British and Estonian examples of *C. elegans* are indistinguishable. The specimens figured by Cramer (1964, pl. 22, fig. 14; pl. 23, figs. 7, 11, 12), and incorrectly identified as *Rhabdochitina conocephala* Eisenack 1934, bear little resemblance to *Conochitina elegans*. Also, I am inclined not to include in this species the two specimens figured by Beju and Danet (1962, pl. 1, figs. 31, 32); they differ from Baltic and British specimens in having sharp basal margins and poorly developed aboral swellings.

Material. Between two thousand and three thousand single tests.

Occurrence. Coston Beds: C16 (uncommon). Glenburrell Beds: C11 (uncommon). Alternata Limestone: C9 (very common). Upper Cheney Longville Flags: C14/b (very common). Acton Scott Beds: C6 (common), C4 (common). *Omnia* Beds: C2/a (very common), C2/b (common), C2/d (common), C1/a–h (common). In Estonia the species occurs in the Kuckers Beds, C₂, the Jewe Beds, D₁, and the Kegel Beds, D₂ (Eisenack 1959a, 1962b). It has been found in many samples of Ostseekalk drift, the type specimens coming from such material from the Hangö–Ekenäs region of South Finland (Eisenack 1959a). Taugourdeau and Jekhowsky (1960) record the species (as *Rhabdochitina conocephala*) in the lower Silurian of the Sahara.

Genus CYATHOCHITINA Eisenack 1955b

Type species. *C. campanulaeformis* (Eisenack 1931), Ordovician, Baltic.

Cyathochitina calix (Eisenack 1931)

Plate 71, figs. 5-7

- 1931 *Conochitina calix* Eisenack, p. 87, pl. 2, fig. 3 (holotype); pl. 4, fig. 14; text-fig. 1.
 1939 *Conochitina calix* Eisenack; Eisenack, p. 137, pl. B, figs. 4, 5.
 1958b *Cyathochitina calix* (Eisenack); Eisenack, p. 397, pl. 2, figs. 26, 27.
 1962a *Cyathochitina calix* (Eisenack); Eisenack, p. 296, pl. 14, figs. 3, 4 (neotype).

Dimensions in microns. (6 specimens measured.)

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>
Range:	255-308	145-174	80-95	96-140	50-69
Mean:	283	159	90	124	58

The average total length of 57 Baltic specimens (Eisenack 1962a) is 299 μ (min. 190 μ , max. 450 μ).

Remarks. At the base of the Hope Shales, *C. calix* and *C. campanulaeformis* (Eisenack 1931) were found together. While most specimens could be allocated with certainty to one or the other of these species, a few were transitional. Most British examples of *C. calix* are somewhat stouter (total length : maximum diameter = 1.5-2.1 : 1) than the Baltic specimens (total length : maximum diameter = 1.9-4.1 : 1) described by Eisenack (1962a).

Material. About twenty-five single tests.

Occurrence. Hope Shales: S25 (abundant). The species has been found (Eisenack 1962a) in the Glaukonitkalk of Estonia and in the *expansus*-Kalk of Dalarna and Öland, Sweden.

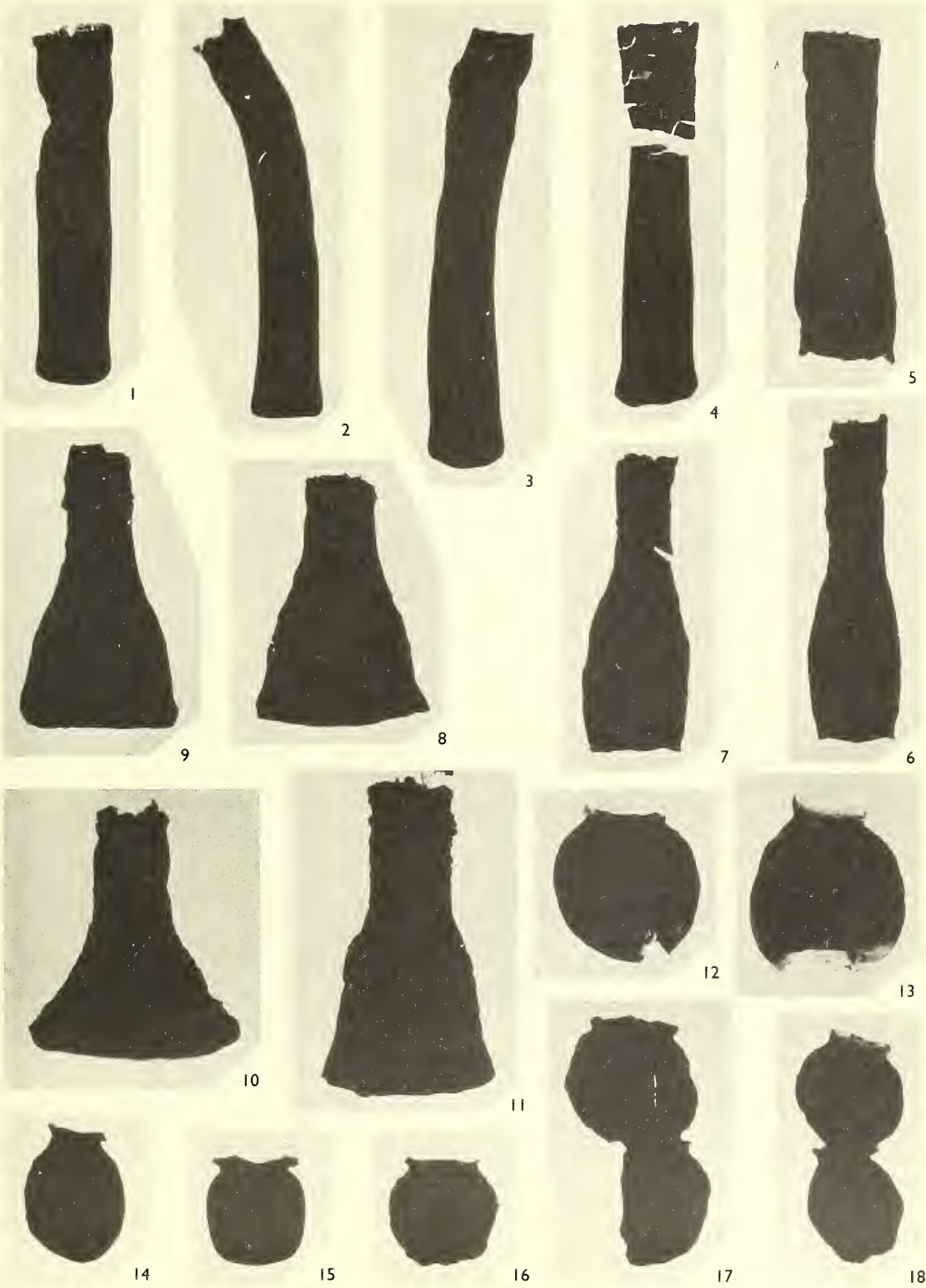
Cyathochitina campanulaeformis (Eisenack 1931)

Plate 71, figs. 8-11

- 1931 *Conochitina campanulaeformis* Eisenack, p. 86, pl. 2, figs. 1, 2 (holotype); pl. 4, figs. 1, 11-13 (non 14).
 1939 *Conochitina campanulaeformis* Eisenack; Eisenack, p. 137, pl. B, figs. 1-3.
 1948 *Conochitina campanulaeformis* Eisenack; Eisenack, p. 112, text-figs. 1, 7-9.
 1955b *Cyathochitina campanulaeformis* (Eisenack); Eisenack, p. 313.

EXPLANATION OF PLATE 71

- Figs. 1-4. *Conochitina elegans* Eisenack. 1, C9/17/2/C, short cylindrical example, $\times 190$. 2, C9/17/2/A, slightly tapering conical example, $\times 190$. 3, C9/17/2/B, $\times 190$. 4, C14/17/2/A, $\times 190$.
 Figs. 5-7. *Cyathochitina calix* (Eisenack). 5, S25/10/4/A, $\times 190$. 6, S25/10/4/B, $\times 190$. 7, S25/10/4/C, $\times 190$.
 Figs. 8-11. *Cyathochitina campanulaeformis* (Eisenack). 8, S21/10/1/2, $\times 190$. 9, S21/10/1/44, $\times 190$. 10, S21/10/2/A, atypical example with short wide chamber, $\times 190$. 11, S21/10/1/45, $\times 190$.
 Figs. 12-13. *Desmochitina minor* Eisenack f. *cocca* Eisenack. 12, C11/45/1/F, $\times 230$. 13, C11/45/1/G, $\times 230$.
 Figs. 14-15, 18. *Desmochitina minor* f. *typica* Eisenack. 14, C16/45/1/A, $\times 230$. 15, C9/45/1/B, $\times 230$. 18, C1/45/1/D, $\times 230$.
 Figs. 16-17. *Desmochitina minor*, typical Llandeilian examples having wide chambers and wide apertures. 16, S11/45/1/B, $\times 230$. 17, S11/45/1/A, $\times 230$.



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1962a *Cyathochitina campanulaeformis* (Eisenack); Eisenack, p. 297, pl. 14, figs. 5 (neotype), 6, 7; text-fig. 3 (neotype).

non 1964 *Cyathochitina campanulaeformis* (Eisenack); Cramer, p. 344, pl. 24, figs. 6–8, 12–15; (figs. 7, 8, 14 = *Cyathochitina kuckersiana* Eisenack).

Diagnosis. Eisenack (1962a, p. 297) gives the following shortened diagnosis. ‘Oral tube cylindrical, chamber bell- or funnel-shaped with relatively sharp basal margin, which not uncommonly is drawn out into a narrow knife-edge rim. Aperture straight. Wall slightly rough, very finely granular, or with extremely fine grooves, like bark.’

Dimensions in microns. (45 specimens measured.)

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>
Range:	170–285	100–202	108–183	40–108	49–70
Mean:	225	160	140	70	60

Eisenack’s (1948) Bohemian specimens measure 190–266 μ in length, his (1962a) Baltic specimens 200–428 (mean 306) μ in length.

Remarks. In shape, the British specimens are similar to the stockier of Eisenack’s (1962a) Baltic specimens; in the former the total length : maximum diameter = 1.18–1.82 : 1 (mean 1.58 : 1); in the latter the ratio is 1.28–2.46 : 1 (mean 1.9 : 1). In size, the British specimens are comparable with the Bohemian specimens (Eisenack 1948) and the smaller of the Baltic specimens. Some individuals from Shropshire are considerably shorter than the shortest Baltic specimens.

In British specimens the base appears to have been a fairly rigid structure. In reflected light it is often seen to have preserved its original circular outline and to have rotated during compression so that it now lies close to, or parallel with, the plane occupied by the remainder of the test. Aboral pores could not be discerned in the isolated bases of several specimens mounted in polar view.

There is little doubt that some of the figured specimens identified by Cramer (1964, pl. 24, figs. 7, 8, 14) as *C. campanulaeformis* are, in fact, examples of *Cyathochitina kuckersiana* (Eisenack 1934); two of these (figs. 7, 14) are fairly close in appearance to *C. kuckersiana* forma *brevis* Eisenack 1962a. The two species may be distinguished readily on the basis of their carinae. The carina of *C. campanulaeformis* is a fairly narrow, sharp rim, whilst that of *C. kuckersiana* is a wide, membranous, skirt-like lateral extension of the basal margin. This distinction (Eisenack, *personal communication*) gives some pure populations of *C. campanulaeformis* and equally pure populations of *C. kuckersiana*; however, since both species show very considerable morphological variation, it also gives populations in which the two species grade into each other.

Material. Several hundred single tests.

Occurrence. Hope Shales: S25 (uncommon), S21 (very common). Weston Beds: S1 (abundant). Betton Beds: S2 (uncommon). Meadowtown Beds: S3 (uncommon), S4 (very common), S5 (very common). In Estonia *C. campanulaeformis* ranges from the Vaginatenkalk, B₃, to the Lyckholm Beds, F₁ (Eisenack 1962a, 1962b); from the Echinospaeritenkalk, C₁, to the Lyckholm Beds it is occasionally very common, while in the Vaginatenkalk it occurs sporadically. It is also known from the *schroeteri*-Kalk of Öland, Sweden (Eisenack 1962a); some chert nodules from the Rhenish Schiefergebirge

(Eisenack 1939); and the Middle Ordovician, d_1 - d_2 , of Bohemia (Eisenack 1948). Taugourdeau (1961) records rare specimens of rather variable shape from the Ordovician or Silurian of Aquitaine and (1962) rare atypical examples from the Middle and Upper Llandoveryan of the Sahara. Benoit and Taugourdeau (1961) list the species in the chitinozoan fauna from the Upper Shale-Grit Formation (Arenigian) of North Africa.

Cyathochitina kuckersiana (Eisenack 1934)

Plate 72, figs. 3-9; Plate 73, fig. 1

1934 *Conochitina kuckersiana* Eisenack, p. 62, pl. 4, fig. 14 (holotype); text-figs. 30 (holotype), 31.

1962a *Cyathochitina kuckersiana* (Eisenack); Eisenack, p. 298, pl. 14, figs. 8 (neotype), 9; text-figs. 4 (neotype), 5.

1964 *Cyathochitina campanulaeformis* (Eisenack); Cramer (pars), pl. 24, figs. 7, 8, 14.

Dimensions in microns. (35 specimens measured.)

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>	<i>Carina width</i>
Range:	146-300	92-202	112-180	50-130	45-60	6-30
Mean:	193	129	143	87	52	20

In size, the British specimens are similar to the smaller of the specimens from the Baltic Kuckers Beds, C_2 , where the total length of 25 specimens ranges from 147 to 360 (mean 253) μ (Eisenack 1962a).

Remarks. In the twenty British populations of this species which have been examined, *C. kuckersiana* (Eisenack 1934) is represented by a large majority of forms closer to

EXPLANATION OF PLATE 72

Fig. 1. *Desmochitina minor* f. *cocca* Eisenack, C11/45/1/A, $\times 230$.

Fig. 2. *Desmochitina minor*, C11/45/4/D, agglomeration of approximately eighty tests, $\times 90$.

Figs. 3-9. *Cyathochitina kuckersiana* (Eisenack). 3, C1/10/14/A, $\times 230$. 4, C1/10/14/B, the translucent membranous carina is of about average width for British examples, $\times 230$. 5, C1/10/14/X, $\times 230$. 6-7, C1/10/14/Zi and C1/10/14/Zii respectively, two aboral polar views of isolated bases showing the wide translucent carinae, $\times 230$; faint concentric striations in the carinae may be distinguished, but the darker radial and oblique radial lines result from folding of this membrane. 8, C1/10/14/U, specimen perforated by circular holes, possibly the result of fungal attack, $\times 570$. 9, C1/10/14/V, three holes immediately above basal margin (the base and carina are missing), $\times 540$. These perforations are described and briefly discussed in the description of this species and in the section devoted to the associated microfossils.

EXPLANATION OF PLATE 73

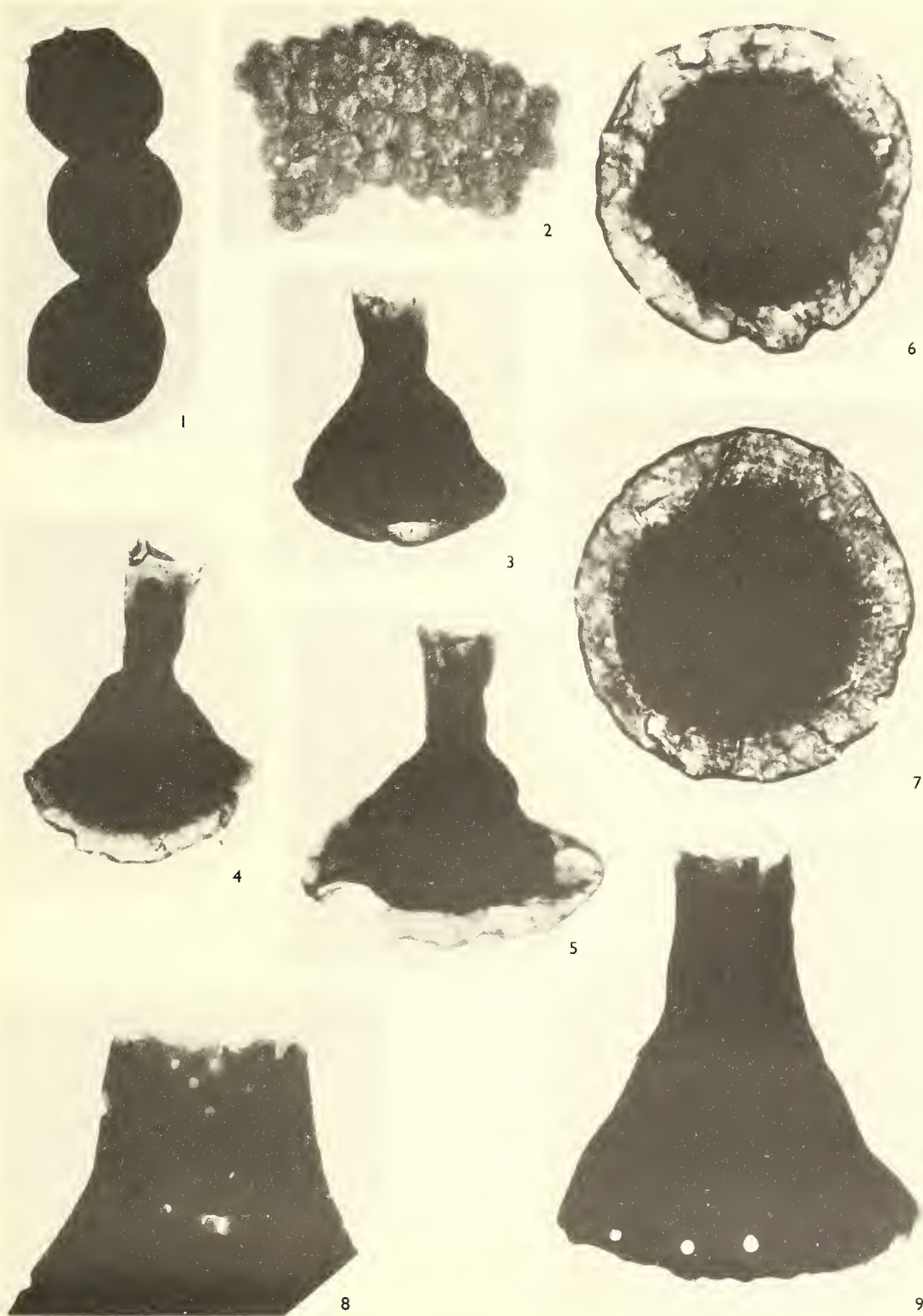
Fig. 1. *Cyathochitina kuckersiana* (Eisenack), C1/10/14/W, aboral polar view of isolated base perforated by numerous circular holes, $\times 415$.

Figs. 2-3. *Lagenochitina capax* sp. nov. 2, C11/12/5/B, $\times 230$. 3, C11/12/5/A, holotype, $\times 230$.

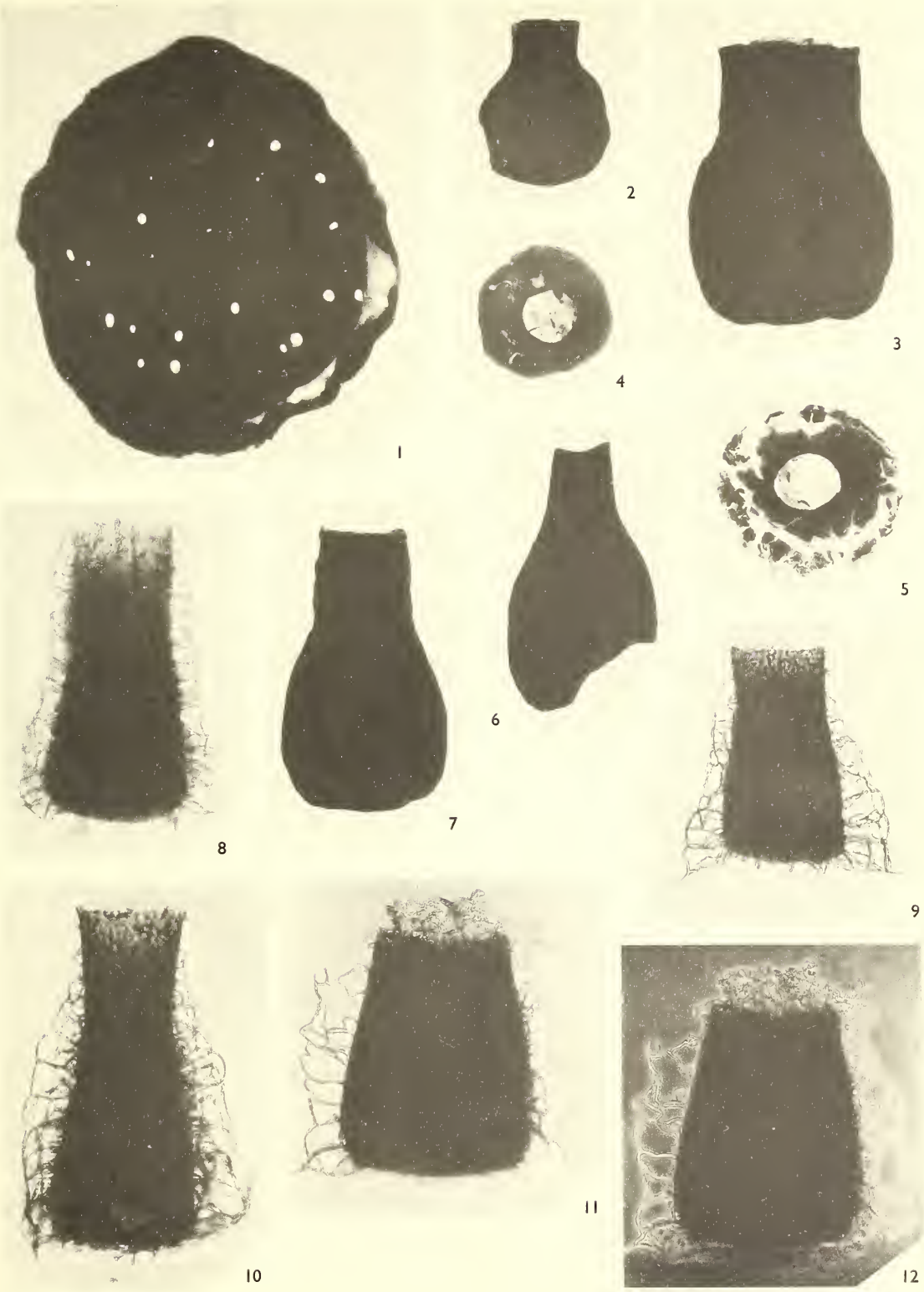
Figs. 4-5. *Hoegisphaera complanata* (Eisenack). 4, C6/65/1/D, oral polar view, $\times 230$. 5, C6/65/1/G, oral polar view clearly showing the aperture, $\times 230$; this specimen was purposely crushed between slide and coverslip in very viscous Canada balsam.

Figs. 6-7. *Lagenochitina baltica* Eisenack. 6, C11/12/3/A, example with slender neck, $\times 230$. 7, C1/12/3/A, example of less common form having wide neck, $\times 230$.

Figs. 8-12. *Hercochitina downiei* sp. nov. 8, C2/b/70/4/C, ornamental elements arranged in rows which show up against translucent oral portion of test wall, $\times 230$. 9, C2/b/70/2/C, holotype, $\times 230$. 10, C2/b/70/4/B, $\times 230$. 11-12, C2/b/70/4/T, $\times 230$; fig. 12 is a phase contrast photograph taken (with the assistance of Dr. L. R. Wilson, Research Professor of Geology, University of Oklahoma) to show somewhat more clearly the nature of the ornamentation.



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C. kuckersiana forma *brevis* Eisenack 1962a than to the holotype and neotype. However, separation of typical *C. kuckersiana* from *C. kuckersiana* forma *brevis* on the basis of the British material would be quite artificial, since they are linked, in each population, by a continuous series of intermediate forms.

The wide, membranous, skirt-like carina is translucent and deep amber in colour, contrasting sharply with the opaque black chamber; in bleached specimens the carina is orange to pale yellow. Faint striations, concentric with the basal margin, have been observed in the carinae of several specimens from Shropshire, but radial strengthenings (reported in some Baltic specimens, Eisenack 1934) are apparently absent. In all samples but one, the width of the carina ranges between 15 and 30 μ (10–20 per cent. maximum diameter); in well-preserved specimens from sample C8/b the carina width does not exceed 12 μ (7.5 per cent. maximum diameter), yet in all other respects these specimens are indistinguishable from those found elsewhere in Shropshire.

As in *C. campanulaeformis* (Eisenack 1931), the base appears to have been fairly rigid. Its original circular outline is often preserved and, during compression, it may have rotated so that it now lies in a plane close to, or parallel with, the longitudinal axis. The bases of twelve specimens were dissected away from the remainder of the tests and mounted for examination in polar view (Pl. 72, figs. 6–7); one of these bases was perforated by a pore situated centrally within the base and measuring about 1 μ in diameter.

The wall is generally smooth, but a more or less pronounced longitudinal ribbing is occasionally developed on the shoulder, the upper flanks, and the lower part of the neck.

The existence of unidentified boring organisms (? fungi) is suggested by the occurrence of holes in the tests of some chitinozoans. In most British populations of *C. kuckersiana*, several specimens are perforated by a number of small circular holes, apparently similar to those in *C. campanulaeformis* from the Baltic (Eisenack 1931, pl. 4, figs. 11, 13) and *C. kuckersiana* forma *brevis* (Eisenack 1962a, pl. 14, fig. 9; holes not mentioned in text). These holes are remarkably uniform in size (4–8 μ in diameter) and distributed irregularly over the test. That they occur selectively in certain species and do not penetrate both sides of the test in completely flattened specimens suggests that the organisms responsible for them were active before fossilization took place. Eisenack (1931) suggested that the holes in *C. campanulaeformis* might be due to microscopic fungi.

Material. Approximately eight thousand single tests.

Occurrence. Coston Beds: C16 (common). Glenburrell Beds: C11 (abundant). Alternata Limestone: C9 (uncommon). Cheney Longville Flags: C8/b–c (abundant), C14/b (very common). Acton Scott Beds: C6 (common), C4 (abundant). *Onnia* Beds: C2/a–d and C1/a–h (abundant). In the Baltic (Eisenack 1962a), *C. kuckersiana* ranges from the Kuckers Beds, C₂, to the Lyckholm Beds, F₁; forma *brevis* is common from the Jewe Beds, D₁, to the Wasalemm Beds, D₃.

Genus DESMOCHITINA Eisenack 1931 emend. 1962a

Type species. *D. nodosa* Eisenack 1931, Ordovician, Baltic.

Desmochitina minor Eisenack 1931

Plate 71, figs. 12–18; Plate 72, figs. 1–2

1931 *Desmochitina?* *minor* Eisenack, p. 93, pl. 3, figs. 9 (holotype), 10, 11.

- 1931 *Desmochitina*? *erinacea* Eisenack, p. 93, pl. 3, fig. 13.
 1931 *Desmochitina*? *cocca* Eisenack, p. 94, pl. 3, figs. 14, 15.
 1931 *Desmochitina amphorea* Eisenack, p. 93, pl. 3, figs. 5, 12.
 1932 *Desmochitina amphorea* Eisenack; Eisenack, p. 267, pl. 12, fig. 6.
 1939 *Desmochitina minor* Eisenack; Eisenack, p. 142, pl. A, figs. 2-5; text-figs. 1-7.
 1948 *Desmochitina minor* Eisenack; Eisenack, p. 115, text-figs. 14, 15.
 1958b *Desmochitina minor* Eisenack; Eisenack, p. 397, pl. 2, figs. 29 (neotype), 30-32.
 1962a *Desmochitina minor* Eisenack; Eisenack, p. 303, pl. 16, figs. 1, 2, 3 (neotype), 4-10
 13-20; pl. 17, figs. 1-9.

Dimensions in microns. (6 Llanvirnian and 40 Caradocian specimens measured.)

		<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>	<i>Apertural diameter</i>
Llanvirnian specimens	Range:	77-106	67-92	78-93	7-14	47-58	53-63
	Mean:	88	77	82	10	50	56
Caradocian specimens	Range:	65-120	55-112	50-115	5-15	26-45	32-53
	Mean:	95	80	75	10	36	45

Remarks. Eisenack (1958b and 1962a) united the four previously named species, *D. minor* Eisenack 1931, *D. erinacea* Eisenack 1931, *D. cocca* Eisenack 1931, and *D. amphorea* Eisenack 1931, regarding them as different forms of a single species, and distinguished the new forms *D. minor* forma *grandicolla* Eisenack 1958b, *D. minor* forma *elongata* Eisenack 1958b, *D. minor* forma *rugosa* Eisenack 1962a, *D. minor* forma *ovulum* Eisenack 1962a, and *D. minor* forma *typica* Eisenack 1958b. Two of Eisenack's forms, *D. minor* f. *typica* and *D. minor* f. *cocca*, have been recognized in Caradocian assemblages from Shropshire. Most specimens allocated to f. *typica* are indistinguishable from some of the examples of *D. minor* from Bohemia (Eisenack 1948, text-figs. 14, 15) and the Ordovician Rhenish Schiefergebirge (Eisenack 1939, text-figs. 1-3, 6), but have smaller, less strongly flaring oral tubes than the specimens of f. *typica* figured by Eisenack (1962a) from the Baltic. However, Eisenack states (1962a, p. 305) that the oral tubes in f. *typica* may be reduced. Baltic and British examples of f. *cocca* are closely similar.

All the examples of *D. minor* from the Llandeilian of Shropshire have relatively wide tests (Pl. 71, figs. 16-17) and closely resemble *D. minor* f. *typica*? (Eisenack 1962a, pl. 16, fig. 10); however, none compares closely with *Desmochitina* sp. (Eisenack 1962a, pl. 16, figs. 11, 12) or *D. lata* Schallreuter 1963.

Material. Several thousand single tests, and chains of up to ten individuals. Agglomerations of up to four hundred loosely attached tests (Pl. 72, fig. 2), superficially similar to those described by Kozłowski (1963), were occasionally found in samples from the basal Caradocian. No evidence was found of an organic-walled envelope around these agglomerations.

Occurrence. (a) *D. minor* f. *typica*: Coston Beds: C16 (common). Glenburrell Beds: C11 (very common). Alternata Limestone: C9 (abundant). Upper Cheney Longville Flags: C14/b (rare). Acton Scott Beds: C6 (common). *Omnia* Beds: C2/b-d and C1/a-h (abundant).

(b) *D. minor* f. *cocca*: Glenburrell Beds: C11 (common).

(c) Llandeilian specimens of *D. minor*: Meadowtown Beds: S8 (rare), S5 and S11 (uncommon).

In the Ordovician of Estonia (Eisenack 1962a) *f. typica* ranges from the Glaukonitkalk, B₂, to the Kuckers Beds, C₂, and also occurs in the Kegel Beds, D₂, the Wesenberg Beds, E, and the Lyckholm Beds, F₁; *f. cocca* occurs in the Reval Beds, C₁, and the Kuckers Beds.

Genus HERCOCHITINA Jansonius 1964 emend.

Type species. *H. crickmayi* Jansonius 1964, Upper Ordovician, Quebec.

Emended diagnosis. Variable conical or cylindroconical tests with ornament of narrow ridges, or spines of uniform length, standing normal to test wall and arranged in longitudinal rows. Spines in each row connected at their tips by a more or less continuous bar running roughly parallel with test wall.

Hercochitina downiei sp. nov.

Plate 73, figs. 8–12

Holotype. Plate 73, fig. 9. Specimen C2/b/70/2/C; *Omnia* Beds, sample C2/b.

Diagnosis. Cylindroconical test. Chamber about two-thirds total length; maximum diameter at base, approximately three-quarters chamber length; base flat or slightly convex, basal margin sharply rounded. Oral tube cylindrical, aperture bearing fringe of fine spines (up to 1.5 μ in length). Ornament of slender simple and wishbone spines, up to two-thirds maximum diameter in length, arranged in 12–16 longitudinal rows, which extend from basal margin to aperture. Bars connecting spine tips continuous, extending whole length of test.

Dimensions in microns. (21 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Apertural diameter	Spine length
Holotype:	152	114	87	38	64	64	up to 54
Range:	135–188	89–119	69–98	35–69	40–62	42–53	up to 59
Mean:	153	101	80	50	50	46	—

Description. Variation in this species is apparently limited to small changes in the size and shape of the test. All spines situated on the chamber are of approximately equal length, whilst those on the oral tube become progressively shorter towards the aperture. Occasionally, two spines in adjacent rows are connected at their tips by an oblique or transverse bar. Generally, however, there is no connexion between spine rows. Spines and the bars connecting them are identical in thickness and texture. Spines on the base are relatively short, up to 6 μ in length, their tips not connected by bars.

Comparison. *H. downiei* sp. nov. is smaller and has a more strongly developed ornament than *H. crickmayi* Jansonius 1964, but it lacks the longitudinal ridges which characterize the type species.

Material. Between four hundred and five hundred single tests.

Occurrence. *Omnia* Beds: C2/a (abundant) and C2/b (abundant).

Genus HOEGISPHAERA Staplin 1961

Type species. *H. glabra* Staplin 1961, Upper Devonian, Alberta.

Hoegisphaera complanata (Eisenack) Jansonius 1964

Plate 73, figs. 4–5

- 1932 *Desmochitina?* *complanata* Eisenack, p. 272, pl. 12, figs. 24 (holotype), 25.
 1959a *Desmochitina?* *complanata* Eisenack; Eisenack, p. 16, pl. 3, fig. 13 (neotype).
 1962 *Desmochitina complanata* Eisenack; Combaz and Poumot, pl. 4, figs. 62, 65.

Dimensions in microns. The following measurements are of ten specimens mounted in polar view. In distorted specimens a maximum and a minimum value were obtained for each measurement; the average of these two values was considered the true value.

	Maximum diameter	Diameter of aperture
Range:	97–127	38–46
Mean:	112	41

Remarks. In polar view, the British examples appear identical to those from the Baltic (Eisenack 1932, 1959a) and North Africa (Combaz and Poumot 1962). Attempts to mount specimens in lateral view proved unsuccessful but, after examining about twenty unmounted specimens in a Petri-dish and rotating them into lateral view, I estimate the chamber length to be about one-third of the maximum diameter (situated centrally) and the collarete length to be only a few microns; it is not known whether the short length of these specimens is wholly original or due partly to compression. The collarete could not be distinguished on specimens examined in polar view and its existence became evident only when the unmounted test was rotated into lateral view.

Material. Approximately one hundred single tests.

Occurrence. Acton Scott Beds: C6 (abundant).

Genus LAGENOCHITINA Eisenack 1931

Type species. *L. baltica* Eisenack 1931, Baltic drift.

Lagenochitina baltica Eisenack 1931

Plate 73, figs. 6–7

- 1931 *Lagenochitina baltica* Eisenack, p. 80, pl. 1, figs. 1 (holotype), 2, 3.
 1959a *Lagenochitina baltica* Eisenack; Eisenack, p. 2, pl. 3, figs. 6 (neotype), 7.

Dimensions in microns. (18 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter
Range:	196–295	130–215	100–152	54–97	40–69
Mean:	248	170	118	65	58

Remarks. Except for some slight discrepancy in size, the British specimens are virtually identical to those from the Baltic. The Silurian specimens from Rumania figured by Beju and Danet (1962, pl. 2, figs. 9, 10), differ in shape subtly, but perhaps critically, from the holotype and neotype.

Material. Forty-five single tests.

Occurrence. Coston Beds: C16 (rare). Glenburrell Beds: C11 (rare). Alternata Limestone: C9 (rare). *Onnia* Beds: C2/a (common), C1/a–d, f–h (rare). The species has been found in Ostseekalk erratics, in the *Diplograptus*-Kalk and in limestones of the Lyckholm Beds, F₁. In Estonia it is known only from the Lyckholm Beds (Eisenack 1962b).

Lagenochitina cylindrica Eisenack 1931

Plate 74, figs. 1–3

1931 *Lagenochitina cylindrica* Eisenack, p. 81, pl. 2, figs. 18, 19 (holotype).

Dimensions in microns. (10 specimens measured.)

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>
Range:	207–331	123–246	108–126	61–143	60–76
Mean:	268	170	113	88	67

Remarks. The chamber forms 53–75 per cent. of the total length, the maximum diameter is 40–55 per cent. of the chamber length (32–38 per cent. total length) and the neck width is half to two-thirds of the maximum diameter. Some British specimens are very similar in size and shape (total length : maximum diameter = 3 : 1) to the Baltic specimens figured by Eisenack (1931, pl. 2, figs. 18, 19); others are shorter and relatively stout (total length : maximum diameter as low as 2·1 : 1). In one British specimen (as in the specimen illustrated in Eisenack 1931, pl. 2, fig. 18) a distinct waist is developed about one-third of the way up the chamber. Three other British specimens have very weakly developed waists located in this same position, whilst in the remaining six specimens no waist can be distinguished and the flanks are quite cylindrical or slightly swollen. A waist appears to be characteristic of this species but it is not developed in all individuals.

Material. Ten single tests.

Occurrence. Hope Shales: S21 (uncommon).

Lagenochitina esthonica Eisenack 1955b

Plate 74, figs. 4–5

1955b *Lagenochitina esthonica* Eisenack, p. 311, pl. 1, figs. 8 (holotype), 9.

1958b *Lagenochitina esthonica* Eisenack; Eisenack, p. 395.

Dimensions in microns.

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>	<i>Apertural diameter</i>
Specimen S21/2/1/A (fig. 4):	987	605	203	382	143	188
Specimen S21/2/1/B (fig. 5):	802	495	180	307	108	150
Holotype (Eisenack 1955b pl. 1, fig. 8):	530	—	194	—	—	—

Remarks. The British specimens of *L. esthonica* Eisenack are larger but more slender than those found by Eisenack (1955b, 1958b) in Estonia. They are similar in length but considerably thinner than the Swedish examples (Eisenack 1955b) from the *expansus*-Kalk. In both British specimens the base is hemispherical, the chamber forms 61 per cent. of the total length and the maximum diameter, lying midway along the chamber, is one-third of the chamber length; the chamber is not slightly conical as in the two specimens figured by Eisenack (1955b). The oral tube is cylindrical and, except for the flaring oral end, 60–70 per cent. of the maximum diameter in width; it is considerably narrower than this in the Estonian and Swedish examples.

Material. Two single tests.

Occurrence. Hope Shales; S21 (rare). Eisenack records the species in the Glaukonitsand, B₁, and the Glaukonitkalk, B_{2a}, of Estonia, and in the *expansus*-Kalk, B_{3a}, of Fjåka, Dalarna, Sweden.

Lagenochitina shelvensis sp. nov.

Plate 74, figs. 7–8

Holotype. Plate 74, fig. 7. Specimen C11/59/1/A (upper test); basal Glenburrell Beds, sample C11.

Diagnosis. Large test. Chamber ovoid to conical, about two-thirds total length; maximum diameter in lower half or middle of chamber, about two-thirds chamber length; base flat to slightly convex, basal margin rounded. Oral tube tapering, cylindrical, or slightly flaring for most of its length; sharply flaring below aperture.

Dimensions in microns. (3 tests measured.)

		Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Apertural diameter
Specimen	{ upper test C11/59/1/A (holotype):	585	365	246	220	146→157	177
		562	370	238	192	146→157	176
	{ lower test:						
Specimen							
C11/59/2/A:		702	432	308	270	193→165	195
(fig. 8)							

EXPLANATION OF PLATE 74

Figs. 1–3. *Lagenochitina cylindrica* Eisenack. 1, S21/12/1/A, ×150. 2, S21/11/1/A, ×150. 3, S21/11/1/B, ×150.

Figs. 4–5. *Lagenochitina esthonica* Eisenack. 4, S21/2/1/A, ×80. 5, S21/2/1/B, ×80.

Figs. 7–8. *Lagenochitina shelvensis* sp. nov. 7, C11/59/1/A, a chain of two tests, ×80; the upper test is the holotype. 8, C11/59/2/A, ×80. Specimen broken in two during mounting; the two parts have been photographed separately.

Figs. 6, 9–10, 12. *Rhabdochitina magna* Eisenack. 6, S8/16/1/C, ×80. 9, S8/16/1/A, ×80. 10, S8/16/1/B, ×80. 12, S21/17/1/A, ×80. The specimens illustrated in figs. 6, 9, and 10 are traversed by parallel splits, which are thought to result from cleavage of the rock, the splits reflecting the orientation of the cleavage plane relative to the original orientation of the specimen in the sediment.

Fig. 11. *Pterochitina* sp., S37/62/1/A, polar view, ×230.

Figs. 13–15, 20. *Rhabdochitina usitata* sp. nov. 13, S21/16/5/A, ×150. 14, S21/16/2/B, ×150. 15, S21/15/5/A, showing stump of basal process, ×230. 20, S21/16/3/B, ×150.

Figs. 16–19. *Rhabdochitina turgida* sp. nov. 16, S21/23/1/B, ×150. 17, S21/16/4/A, ×150. 18, S21/16/4/B, ×150. 19, S21/23/1/A, holotype, ×150.



JENKINS, Ordovician chitinozoa

Comparison. In size and general shape *L. shelvensis*, sp. nov. compares closely with *L. bohemica* Eisenack 1948, but lacks the pronounced apertural thickening of typical members of that species. Eisenack (*personal communication*) states that he would not include these specimens in *L. bohemica* and that they appear to be a new species, perhaps related to *L. bohemica*. It will not be possible to precisely define and distinguish *L. bohemica* Eisenack and *L. shelvensis* sp. nov. until numerically larger populations of both species have been found.

Material. One single test, one chain of two tests, and several fragments.

Occurrence. Glenburrell Beds: C11 (rare).

Lagenochitina capax sp. nov.

Plate 73, figs. 2–3

Holotype. Plate 73, fig. 3. Specimen C11/12/5/A; basal Glenburrell Beds, sample C11.

Diagnosis. Swollen cylindrical chamber, slightly wider than long, about two-thirds total length; shoulder pronounced; maximum diameter midway along chamber; base flat or almost so, basal margin rounded. Neck distinct, wider than long, cylindrical, half to two-thirds maximum diameter in width. Aperture straight.

Dimensions in microns.

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Neck diameter</i>	<i>Apertural diameter</i>
Holotype:	209	140	150	69	100	104
Specimen C11/12/5/B:	122	88	95	34	46	50

Remarks. The outer surface of the test wall is rough but lacks processes; this texture may not be original. *L. capax* sp. nov. is quite distinct.

Material. Two single tests.

Occurrence. Glenburrell Beds: C11 (rare).

Genus PTEROCHITINA Eisenack 1955a

Type species. *P. perivelata* (Eisenack 1937), Silurian, Baltic.

Diagnosis. 'Chitinozoa in which the chamber width equals or exceeds the test length, and bearing a circular wing-like membrane' (Eisenack 1955a, p. 177).

Pterochitina sp.

Plate 74, fig. 11

Dimensions. Owing to slight distortion of the test, a minimum and maximum value were obtained for each dimension.

	<i>Over-all diameter (including membrane)</i>	<i>Diameter of chamber</i>
Specimen S37/62/1/A:	136 × 165	73 × 85

Remarks. The test consists of a dark opaque chamber lying centrally within a translucent, apparently thin-walled membrane. In polar view, the chamber and membrane are almost circular in outline (slightly distorted during fossilization) and the diameter of the chamber is about half that of the over-all diameter. Since the test is poorly preserved and has been examined only in polar view, the relationship of the chamber to the membrane has not been determined; in particular, it is not known how, and where, the two are attached. The aperture was not discernible owing to the opaque nature of the chamber wall; this is also the case in some examples of *P. perivelata* (Eisenack 1955a).

Comparison. The British specimens are smaller than *P. makroptera* Eisenack 1959a (p. 17; over-all diameter of twelve specimens: min. 180, max. 347) and lack concentric striations on the outer membrane. They are similar in size to *P. retracta* Eisenack 1955b and *P. perivelata*, but apparently lack the umbrella-like outer membrane of the former species and have relatively smaller chambers than the latter. For the present, the British form is designated *Pterochitina* sp.

Material. One complete specimen and several fragments.

Occurrence. Stapeley Shales: S37 (rare).

Genus RHABDOCHITINA Eisenack 1931

Type species. *R. magna* Eisenack 1931, Baltic drift.

Rhabdochitina magna Eisenack 1931

Plate 74, figs. 6, 9–10, 12

- 1931 *Rhabdochitina magna* Eisenack, p. 90, pl. 3, figs. 16, 17, 18 (holotype); text-figs. 3–5.
 1939 *Rhabdochitina magna* Eisenack; Eisenack, p. 145, pl. B, fig. 9.
 1960 *Rhabdochitina magna* Eisenack; Taugourdeau and Jekhowsky, p. 1230, pl. 9, fig. 132 (non pl. 10, fig. 133).
 1961 *Rhabdochitina magna* Eisenack; Benoit and Taugourdeau, p. 1411, pl. 5, fig. 54 (non pl. 5, fig. 53).
 1962a *Rhabdochitina magna* Eisenack; Eisenack, p. 292, pl. 14, fig. 1; pl. 15, fig. 5; text-fig. 1.

Dimensions in microns. (1 Llanvirnian and 15 Llandeilian specimens measured.)

		Total length	Maximum diameter	Apertural diameter
Llanvirnian specimen (S21/17/1/A):		562	77	39
Llandeilian specimens	Range:	750–909	110–142	90–139
	Mean:	823	131	115

The original dimensions given for the species (Eisenack 1931) were: total length 500–1,000 μ , width 80–100 μ . The mean total length and mean width of eight complete Baltic specimens (Eisenack 1962a) are 1,100 μ (max. 1,350, min. 874) and 93 μ (max. 113, min. 80), respectively.

Remarks. Typical examples of *R. magna* were found in only two samples. Those from the lower Meadowtown Beds (S8) are wider than the Baltic examples and generally somewhat shorter, while the sole example from the Hope Shales (S21) is relatively small. The base shows the same variety of shape as it does in the Baltic examples (Eisenack

1962a). The specimens from sample S8 (Pl. 74, figs. 6, 9–10) are traversed by parallel splits, which are thought to result from cleavage of the rock, the splits reflecting the orientation of the cleavage plane relative to the original orientation of the specimen in the sediment.

Material. Several hundred single tests.

Occurrence. Hope Shales: S21 (rare). Meadowtown Beds: S8 (abundant). Short wide atypical forms of *R. magna* were found in the Hope Shales (S21, S36) and the Meadowtown Beds (S8, S3). Typical examples of *R. magna* are occasionally very common (Eisenack 1962a) in the Ostseekalk and also occur (Eisenack 1962b) in B₃ and C₁ of Estonia. Atypical forms occur in the Vaginatenkalk of Reval, B_{3y}, and the Echinospaeritenkalk of Reval, C₁, the *Chasmops*-Kalk (Caradocian) of Böda, Öland, the Ordovician Rhenish Schiefergebirge, and the Middle Ordovician, D_y, of Bohemia. In Estonia, a whole range of forms can only be described as *R. cf. magna* (Eisenack 1962a). Taugourdeau and Jekhowsky (1960) give the stratigraphical range of the species in the Sahara as Ordovician (zone 2) to Silurian (zone 3), and Benoit and Taugourdeau (1961) record it at nine horizons in the Arenigian of North Africa. It is evident from the specimens identified as *R. magna* and figured by Taugourdeau and Jekhowsky (1960), and Benoit and Taugourdeau (1961) that these authors interpret *R. magna* more widely than does Eisenack.

Rhabdochitina turgida sp. nov.

Plate 74, figs. 16–19

Holotype. Plate 74, fig. 19. Specimen S21/23/1/A; basal Hope Shales, sample S21.

Diagnosis. Stout, slightly swollen cylindrical test; maximum diameter central, one-third to half total length. Base wide, concave or flat; basal margin rounded. Wall smooth.

Dimensions in microns. (10 specimens measured.)

	Total length	Maximum diameter	Apertural diameter
Holotype:	231	87	46
Range:	146–362	69–131	38–81
Mean:	252	95	55

Description. From its widest part, the test narrows slightly towards the base and towards the straight aperture, both of which are between half and three-quarters of the maximum diameter in width.

Comparison. This species differs from short, wide examples of *R. striata* Eisenack (1958b, pl. 2, fig. 25) only in its lack of longitudinal striations. Typical examples of *R. gallica* Taugourdeau 1961 are widest aborally, although two of Taugourdeau's figured specimens (1961, pls. 4 and 5, figs. 72, 74) appear to be quite cylindrical.

Material. Twenty-five single tests.

Occurrence. Hope Shales: S21 (uncommon), S36 (rare). Weston Beds: S1 (rare). Meadowtown Beds: S3 (rare).

Rhabdochitina usitata sp. nov.

Plate 74, figs. 13–15, 20; Plate 75, fig. 1

Holotype. Plate 75, fig. 1. Specimen S21/16/2/A; basal Hope Shales, sample S21.

Diagnosis. Stout, cylindrical or weakly conical test; maximum diameter one-fifth to one-third total length. Base hemispherical. Aperture straight, 60–80 per cent. maximum diameter in width. Wall smooth.

Dimensions in microns. (35 specimens measured.)

	<i>Total length</i>	<i>Maximum diameter</i>	<i>Apertural diameter</i>	<i>Basal process diameter</i>
Holotype:	418	108	70	—
Range:	262–578	85–130	42–93	30–43 (4 specimens measured)
Mean:	414	112	75	36 (4 specimens measured)

Description. The base is invariably hemispherical, and approximately one specimen in five appears to have borne a stout process attached to the centre of the base (fig. 15); at its origin, this process is 26–37 per cent. of the maximum diameter in width. Generally only the scar of its attachment remains, and it has not been found complete.

Comparison. In general shape *R. usitata* sp. nov. is similar to *R. gallica* Taugourdeau 1961, but the latter has no basal process and its base may be flat. *R. turgida* sp. nov. is readily distinguished from *R. usitata* sp. nov. by its swollen cylindrical test and its flat or concave base; these two species sometimes occur together but no intermediate forms have been found. *R. usitata* sp. nov. is distinguished from *R. magna* Eisenack 1931 by its shorter, sometimes weakly conical test, and by its invariably hemispherical base.

Material. Several hundred single tests.

Occurrence. Hope Shales: S25 (rare), S21 (abundant), S36 (uncommon). Weston Beds: S1 (uncommon). Betton Beds: S2 (uncommon). Meadowntown Beds: S8 (uncommon), S3 (common), S11 (rare). Glenburrell Beds: C11 (rare). Acton Scott Beds: C4 (uncommon). *Onnia* Beds: C2/a (uncommon), C2/b–c (rare).

Genus SIPHONCHITINA gen. nov.

Type species. *S. formosa* sp. nov., Hope Shales, Llanvirnian, Shropshire.

Diagnosis. Chitinozoa with variably shaped, generally slender tests. The test wall consists of two layers which separate at or near the basal margin, the inner layer forming the convex or hemispherical base, the outer layer extending aborally beyond the base as a hollow, cylindrical or flaring, open-ended tube, the siphon.

Remarks. The diagnostic feature of *Siphonochitina* gen. nov. is the separation of the inner and outer wall layers to form, respectively, the base and the siphon. This characteristic appears to be common to a group of otherwise similar species; it is recognizable even in distorted material, and generic separation based upon it should prove reasonably

objective. A chamber and a neck are usually distinguishable, but only occasionally is their junction sharply defined, e.g. *Siphonochitina pellucida* (Benoit and Taugourdeau) comb. nov. Because of the frequent difficulty in recognizing the junction of the neck and the chamber, the maximum diameter is sometimes more reliably expressed, in diagnoses, as a percentage of the total length (excluding siphon) than as a percentage of the chamber length. The test wall is smooth. The two wall layers adhere closely, and are usually distinguishable only aborally, where they separate. The outer layer forming the siphon is commonly translucent, relatively thin, and often folded or damaged. The inner layer, especially aborally, is more opaque and apparently thicker than the outer layer. In some species (*S. formosa* sp. nov., *S. robusta* sp. nov.) a short process is attached to the centre of the base; it lies within the siphon and is directed aborally. The aperture is straight. The structure at the aboral end of the test in *Desmochitina* may prove to be quite different to that in *Siphonochitina*.

The following species are assigned to *Siphonochitina*: *S. formosa* sp. nov., *S. tenuicollis* sp. nov., *S. clavata* sp. nov., *S. robusta* sp. nov., and, with reservations, *S. pellucida* (Benoit and Taugourdeau 1961) comb. nov. *Desmochitina? gigantea* Eisenack 1948 possibly belongs here but the description and illustrations of this species do not indicate the existence of two wall layers. Also, certain forms presently assigned to *Eremochitina* Benoit and Taugourdeau 1961 may prove to belong in *Siphonochitina*.

Siphonochitina formosa sp. nov.

Plate 75, figs. 2–5; text-fig. 9

Holotype. Plate 75, fig. 2. Specimen S36/1/8/A; upper Hope Shales, sample S36.

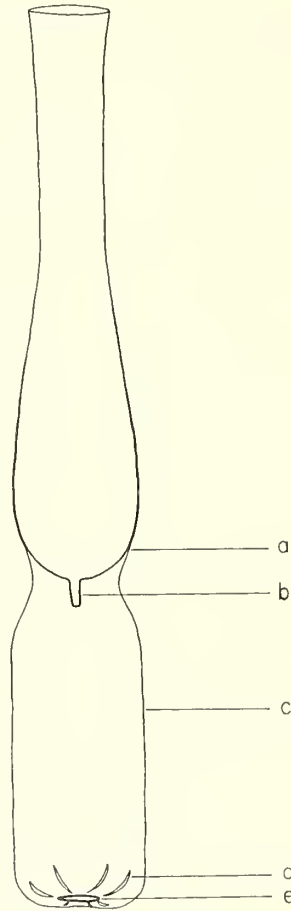
Diagnosis. Gently tapering, slender conical chamber, 50–60 per cent. total length (excluding siphon); maximum diameter (of chamber) in lower part of chamber, 15–35 per cent. total length (excluding siphon). Oral tube cylindrical or slightly flaring, half to two-thirds maximum diameter (of chamber) in width. Siphon cylindrical, similar to chamber in length and width; sharply constricted at its distal end to a circular opening surrounded by a dark opaque ring, 15–20 μ in diameter; wall of siphon apparently thin. A small opaque cylindrical or conical process, about 10 μ in length, firmly attached to centre of base.

Dimensions in microns. (23 specimens measured.)

	Total length	Chamber length	Maximum diameter (of chamber)	Oral tube length	Oral tube diameter	Siphon length	Siphon diameter
Holotype:	380	142	54	88	30	150	55
Range:	250–452	90–182	48–54	60–134	23–30→30–40	90–190	46–62
Mean:	373	140	51	96	27→34	137	55

Description. While a large majority of specimens have conical chambers, a few have swollen cylindrical chambers in which the maximum diameter lies centrally; transitional forms link these with the holotype. The base, clearly visible through the siphon wall, is strongly or slightly convex. Commonly, the neck and chamber merge gradually, but sometimes their junction is abrupt (Pl. 75, fig. 5). The prosome is generally present and clearly

visible, often lying at the base of the neck as a short, opaque, cylindrical plug. Occasionally, up to twenty faint, narrow transverse striations occur fairly evenly distributed along the length of the neck; structurally it is not known whether these striations lie



TEXT-FIG. 9. *Siphonochitina formosa* gen. et sp. nov. Diagrammatic lateral view of test, $\times 320$. *a*, point of separation of the inner and outer wall layers. *b*, basal process. *c*, siphon. *d*, folds disposed radially about the distal opening of the siphon. *e*, dark ring around the distal opening of the siphon.

within the test wall or are part of the prosome. The collarete is often paler, and sometimes more strongly flaring than the neck; the aperture is straight. The siphon is remarkably large, commonly as long as the chamber and generally slightly wider than the maximum diameter of the chamber. The dark ring around the distal opening is considerably narrower than the oral aperture, suggesting that individuals in chains were not connected aperture-to-base. The siphon is pale yellow-brown and translucent, and folds, radially disposed about the distal opening, are common. The small process on the base

shows clearly through the wall of the siphon. It is remarkably constant in size, invariably opaque, and is directed aborally along the longitudinal axis of the test.

Comparison. The size of the siphon and the presence of a small basal process distinguish *S. formosa* sp. nov.

Material. Five hundred to six hundred single tests.

Occurrence. Hope Shales: S36 (abundant).

Siphonochitina tenuicollis sp. nov.

Plate 75, figs. 6–7

Holotype. Plate 75, fig. 7. Specimen S21/1/5/A; basal Hope Shales, sample S21.

Diagnosis. Slender, swollen cylindrical or conical chamber, about half total length (excluding siphon); maximum diameter midway along chamber or near base, 20–25 per cent. total length (excluding siphon). Slender, cylindrical, or slightly tapering neck, 40–55 per cent. maximum diameter in width. Siphon about one-fifth to one-third chamber length, cylindrical or flaring, half to four-fifths chamber diameter in width.

Dimensions in microns. (15 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Siphon length	Siphon diameter
Holotype:	322	150	54	120	25 → 20	52	24 → 47
Range:	223–337	90–157	50–60	80–181	23–33 → 19–33	31–73	24–44 → 28–52
Mean:	291	127	53	110	26 → 26	50	32 → 40

Description. The chamber and neck may merge or, less commonly, they may meet abruptly. The neck is generally cylindrical, sometimes slightly tapering. The base is convex and there is apparently no basal process. The siphon may be cylindrical or flaring, or a composite of both, and is always considerably wider than the neck. Owing to poor preservation the siphon is generally distorted or torn, and I was unable to determine whether the distal opening of the siphon is constricted and enclosed by an opaque ring, as it is in *S. formosa* sp. nov.

Comparison. *S. tenuicollis* sp. nov. has a much shorter siphon and a somewhat narrower neck than *S. formosa* sp. nov., and apparently lacks a basal process; however, the two species are probably closely related.

Material. Twenty-five single tests.

Occurrence. Hope Shales: S25 (uncommon), S21 (common).

Siphonochitina cf. *pellucida* (Benoit and Taugourdeau) comb. nov.

Plate 75, figs. 9–11

Dimensions in microns. (4 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter	Siphon length	Siphon diameter
Range:	167–224	83–116	65–73	50	50	20–58	38–58
Mean:	184	101	70	50	50	35	45

Remarks. The British specimens compare closely with those described by Benoit and Taugourdeau (1961, p. 1408, pl. 3, figs. 31–36; pl. 4, fig. 37) from the Lower Ordovician of the Sahara, but they have slightly less swollen chambers than the latter. The siphon may be a cylindrical tube about half as long as the body chamber and considerably narrower than the neck (fig. 10), as in the Saharan specimens, or it may be strongly flaring, only about one-fifth as long as the chamber and slightly wider than the neck (fig. 11). I suspect that the ‘tunique semblant envelopper tout le Chitinozoaire, et plus ou moins séparée de la copula’ (Benoit and Taugourdeau 1961, p. 1408, pl. 3, figs. 31, 32) represents the outer layer of a two-layered test wall, and also forms the siphon. Too few specimens were found to decide whether, on the basis of their wide flaring siphons, some of the British specimens should be assigned to a new species. For the present, all are referred to *S. cf. pellucida* Benoit and Taugourdeau 1961.

Comparison. This form is readily distinguished from species of *Desmochitina* by its more elongate test and its well-developed cylindrical neck. The short swollen chamber and its abrupt junction with the neck distinguish *S. pellucida* from other species of *Siphonochitina*.

Material. Seven single tests.

Occurrence. Glenburrell Beds: C11 (uncommon). Typical *S. pellucida* is very common in the Hamra Quartzites and the Lower Shale-Grit Complex of the Sahara, in samples dated by graptolites as Lower Arenig.

Siphonochitina clavata sp. nov.

Plate 75, figs. 8, 12–13

Holotype. Plate 75, fig. 8. Specimen C11/1/6/A; basal Glenburrell Beds, sample C11.

Diagnosis. Gently tapering, elongate conical chamber, about two-thirds total length; maximum diameter close to base, 20–30 per cent. total length. Oral tube cylindrical

EXPLANATION OF PLATE 75

Fig. 1. *Rhabdoclitina usitata* sp. nov., S21/16/2/A, holotype, $\times 150$.

Figs. 2–5. *Siphonochitina formosa* gen. et sp. nov. 2, S36/1/8/A, holotype, $\times 150$. 3, S36/1/9/A, $\times 150$. 4, S36/1/8/B, $\times 150$. 5, S36/1/8/C, example with considerably longer siphon than chamber, $\times 150$.

Figs. 6–7. *Siphonochitina tenuicollis* gen. et sp. nov. 6, S21/1/3/A, $\times 150$. 7, S21/1/5/A, holotype, $\times 150$.

Figs. 9–11. *Siphonochitina cf. pellucida* (Benoit and Taugourdeau) comb. nov. 9, C11/1/7/C, $\times 230$. 10, C11/1/7/A, example with cylindrical siphon, $\times 230$. 11, C11/1/7/D, $\times 230$.

Figs. 8, 12–13. *Siphonochitina clavata* gen. et sp. nov. 8, C11/1/6/A, holotype, $\times 230$. 12, S2/1/10/A, $\times 230$. 13, C11/1/6/D, $\times 230$.

Figs. 14–18. *Siphonochitina robusta* gen. et sp. nov. 14, S21/29/5/B, $\times 150$. 15, S21/29/5/C, $\times 150$. 16, S21/29/5/A, $\times 150$. 17, S21/29/4/A, holotype, $\times 150$. 18, S36/29/6/I, $\times 230$; the siphon has been dissected away to show the base and the basal process.

Figs. 19, 21–22. *Sphaerochitina vulgaris* sp. nov. 19, S21/5/1/H, holotype, $\times 230$. 21, S21/5/1/C, $\times 230$. 22, S21/5/1/D, $\times 230$; this example bears small spines and cones at the aboral end of the chamber.

Figs. 20, 23–24. *Sphaerochitina actonica* sp. nov. 20, C6/54/3/C, holotype, $\times 230$. 23, C6/54/3/A, $\times 230$. 24, C6/54/3/F, $\times 230$; a single photograph; the upper part of the oral tube has broken away from the remainder of the test.



JENKINS, Ordovician chitinozoa

for most of its length, slightly flaring orally, about two-thirds maximum diameter in width. Siphon short, about one-tenth total length, sharply flaring.

Dimensions in microns. (3 Llandeilian and 4 Caradocian specimens measured.)

	<i>Total length</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>	<i>Siphon length</i>	<i>Siphon diameter</i>
Holotype:	228	131	65	77	42	20	45 → 55
Llandeilian specimens							
Range:	248+ -381	123-200	82-90	95+ -154	—	27+ -46	65 → 77
Caradocian specimens							(one specimen)
Range:	228-278	131-181	58-77	77-78	38-54	20-26	35-50 → 45-72

Description. The base is slightly convex and a basal process is lacking. The chamber merges with the neck, the collarete is flaring, and the aperture is straight. Proximally, the siphon is about as wide as the cylindrical portion of the oral tube; it flares sharply throughout its length, and at its distal end it may be almost as wide as the widest part of the chamber. Little is known of the variation shown by this species since only seven specimens have been found.

Comparison. Some specimens of *Desmochitina? gigantea* Eisenack (1948, pl. 1, figs. 1-4) are similar in shape to *S. clavata* sp. nov. but are much larger and may have a prominent ledge (Halskrause) developed on the shoulder.

Material. Seven single tests.

Occurrence. Betton Beds: S2 (rare). Glenburrell Beds: C11 (rare).

Siphonochitina robusta sp. nov.

Plate 75, figs. 14-18, text-fig. 10

Holotype. Plate 75, fig. 17. Specimen S21/29/4/A; basal Hope Shales, sample S21.

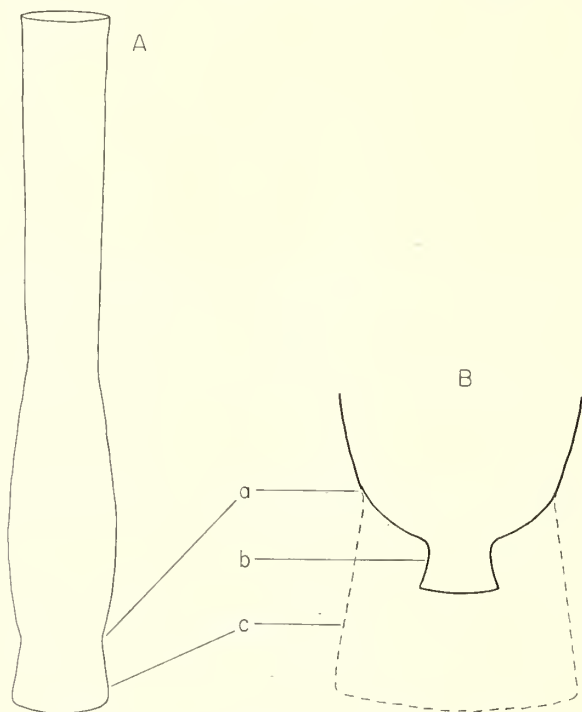
Diagnosis. Large slender test. Chamber elongate, conical or swollen cylindrical, about half total length (excluding siphon); maximum diameter midway along chamber or close to base, 15-22 per cent. total length (excluding siphon). Oral tube cylindrical or flaring. Siphon short, wide, cylindrical or sharply flaring. Stout process attached to centre of base.

Dimensions in microns. (45 specimens measured.)

	<i>Total length (excluding siphon)</i>	<i>Chamber length</i>	<i>Maximum diameter</i>	<i>Oral tube length</i>	<i>Oral tube diameter</i>	<i>Siphon length</i>	<i>Siphon diameter</i>
Holotype:	531	223	96	308	69 → 85	65	77
Range:	362-616	150-308	77-98	208-385	58-69 → 58-85	20-65	40-85
Mean:	489	229	88	297	62 → 66	40	64

Description. The chamber and neck sometimes merge so gradually that their lengths cannot be measured precisely. Where their junction is more abrupt the maximum

diameter is seen to be 25–40 per cent. of the chamber length. The base is convex or hemispherical, but in complete specimens it is hidden by the siphon, which in the present material is always opaque. When cylindrical, the oral tube is about three-quarters of the maximum diameter in width; when flaring, it is about three-quarters of the maximum



TEXT-FIG. 10. *Siphonochitina robusta* gen. et sp. nov. A, Lateral view of intact test, $\times 190$. B, Diagram to illustrate the structure at the aboral end of the test, $\times 450$. a, point of separation of the inner and outer wall layers. b, basal process. c, siphon.

diameter in width near the chamber, and nearly as wide as the maximum diameter at its oral end. In general, the collarette is slightly translucent and contrasts with the opaque neck; the aperture is straight. The structure at the aboral end of the test (text-fig. 10) has been interpreted with some difficulty, owing to the opaque nature of the test wall. The siphon rises from the basal margin and extends aborally as a short, wide, cylindrical or flaring tube with a straight, smooth termination. The close and persistent similarity between the terminal diameter of the siphon and the diameter of the aperture suggests that these, at one time, may have been the points of contact between individuals in chains. When the siphon has not been preserved intact, or when it is removed (Pl. 75, fig. 18), a stout process can be seen attached to the centre of the base. This process is directed aborally and its distal end is often broken. Populations of *S. robusta* sp. nov. from samples S21 and S36 show the same morphological variation.

Material. Approximately eight hundred single tests.

Occurrence. Hope Shales: S21 (abundant), S36 (abundant). Glenburrell Beds: C11 (rare).

Genus SPHAEROCHITINA Eisenack 1955a

Type species. *S. sphaerocephala* (Eisenack 1932), Silurian drift, Baltic.

Diagnosis. 'Chitinozoa with roughly cylindrical neck and conical, spherical or broad fungiform chamber. Wall smooth, bearing minute tubercles, or covered with closely spaced, tiny spines; large processes absent' (Eisenack 1955a, p. 162).

Remarks. Part of the original diagnosis, 'dicht stehenden', has been translated into English by Collinson and Scott (1958) and Dunn (1959) as 'thick, erect', and into French by Taugourdeau and Magloire (1963 MS.) as 'très près les unes des autres'. The correct English translation would appear to be 'closely spaced'.

Sphaerochitina vulgaris sp. nov.

Plate 75, figs. 19, 21, 22; text-fig. 11

Holotype. Plate 75, fig. 19. Specimen S21/5/1/H; basal Hope Shales, sample S21.

Diagnosis. Small cylindroconical test. Chamber about half total length; maximum diameter at base, half to two-thirds total length; basal margin sharp, base flat or slightly convex. Neck cylindrical, half to two-thirds maximum diameter in width. Collarette translucent, occasionally flaring. Wall smooth or bearing small cones and, rarely, a few short simple spines.

Dimensions in microns. (12 specimens measured.)

	<i>Total length</i>	<i>Maximum diameter</i>	<i>Neck diameter</i>	<i>Apertural diameter</i>
Holotype:	111	71	44	50
Range:	108–135	68–87	41–50	41–48
Mean:	119	78	44	44

Description. The chamber and neck may meet abruptly and be sharply distinct, or they may merge so that their junction cannot be precisely located and reliable measurements of their lengths cannot be taken. The aperture is usually straight but occasionally it bears a fringe of small cones; it is half to two-thirds of the maximum diameter in width. In a small majority of specimens, the test walls are ornamented with few or many small cones (up to $1\ \mu$ in length) and, uncommonly, very small spines (up to $2.5\ \mu$ in length). These processes are most strongly developed and occur most frequently near the basal margin; orally they become progressively smaller and less common.

Comparison. *S. fungiformis* (Eisenack 1931) differs from *S. vulgaris* sp. nov. in having a fungiform test, a proportionately longer neck and a rounded basal margin; in *S. nodulosa* Collinson and Scott 1958 the ornament consists of thorn-like spines, which sometimes occur on the neck, or rounded nodes. In *S. collinsoni* Dunn 1959 the chamber

is more depressed than in the new species, the neck is relatively longer and narrower, and the processes are larger.

Material. Fifty-five single tests.

Occurrence. Hope Shales: S21 (common).

Sphaerochitina actonica sp. nov.

Plate 75, figs. 20, 23, 24; text-fig. 12

Holotype. Plate 75, fig. 20. Specimen C6/54/3/C; basal Acton Scott Beds, sample C6.

Diagnosis. Small fungiform test. Chamber wide, about 60 per cent. total length; maximum diameter at base, 120–140 per cent. chamber length; basal margin bluntly rounded;

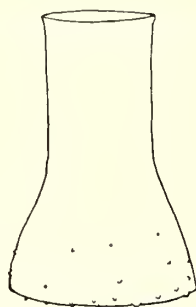


Fig. 11

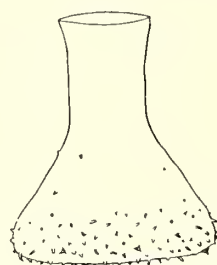


Fig. 12

TEXT-FIG. 11. *Sphaerochitina vulgaris* sp. nov. Lateral view of an ornamented test illustrating the nature, size, and distribution of the processes, $\times 325$.

TEXT-FIG. 12. *Sphaerochitina actonica* sp. nov. Lateral view of an ornamented test illustrating the nature, size, and distribution of the processes, $\times 310$.

base flat or convex. Neck cylindrical or slightly flaring, one-third to half maximum diameter in width; collarette often strongly flaring. Wall smooth or bearing numerous small simple and wishbone spines, restricted to the chamber and concentrated around the basal margin.

Dimensions in microns. (6 specimens measured.)

	Total length	Chamber length	Maximum diameter	Oral tube length	Oral tube diameter
Holotype:	110	62	85	48	29 $\rightarrow$ 35
Range:	95–118	56–67	75–90	41–49	29–35 $\rightarrow$ 35–44
Mean:	104	62	85	44	32 $\rightarrow$ 38

Description. In general the chamber and neck are distinct, and their lengths can be measured precisely. The nature of the aperture is not known with certainty, since only specimens with damaged collarettes have been found; in two slightly damaged specimens, however, the aperture appears to be straight. The spines have sharp or blunt tips and are up to 4μ in length. They are largest and most closely spaced near the basal margin, whilst on the upper flanks they are minute and very scarce; the neck is quite smooth.

Comparison. *S. pistilliformis* (Eisenack 1931) and *S. fungiformis* (Eisenack 1931) lack wishbone spines and have proportionately longer necks (two-thirds of the total length) than *S. actonica* sp. nov. *S. schwalbi* Collinson and Scott 1958 has a slightly shorter neck than *S. actonica* sp. nov. and a dense ornament of very short, simple spines covering the whole test.

Material. Several hundred single tests.

Occurrence. Acton Scott Beds: C6 (abundant).

ASSOCIATED MICROFOSSILS

Several other kinds of acid-resistant microfossils, including graptolite siculae, scolecodonts, acritarchs, and the organic linings of foraminifera, were found in association with the chitinozoans. These associated microfossils have not been studied systematically but are described briefly below. Their state of preservation is often excellent.

Graptolite siculae. Siculae and other graptolite fragments occur in various sediments throughout the Ordovician successions of the Shelve and Caradoc districts. Surprisingly, very large numbers were found in several samples from horizons in the Caradoc succession where graptolites in the form of macrofossils are exceedingly rare or have not been recorded; in the Shelve area siculae were not found in the Weston Beds. In some of the more well-preserved material, the prosicula, metasicula, and virgella are clearly distinguishable.

Scolecodonts. Scolecodonts, the jaws of polychaete worms, occur throughout the two Ordovician successions in virtually all types of sediment, except volcanic ash. A considerable variety of jaws was found but no attempt has been made to identify them. Scolecodonts are relatively resistant to oxidation. In weathered samples they are preserved noticeably better than the other groups of organic-walled microfossils (including the Chitinozoa), and they are the least readily bleached in several oxidizing agents, including Schultze's solution, concentrated nitric acid, fuming nitric acid, and sodium hypochlorite.

Acritarchs. Acritarchs have been found at more than twenty horizons between the base of the Llanvirnian and the top of the Caradocian. In some cases their preservation is excellent (samples C14/b and C1/a-h) but, since they are readily destroyed by carbonization and oxidation, they are not found in cleaved or greatly weathered sediments. Those acritarchs which have been examined and identified were retained on the 300-mesh sieve and represent only the larger size-fractions of much larger acritarch assemblages. They belong to five genera:

1. *Baltisphaeridium* Eisenack 1958a emend. Downie and Sarjeant 1963.

Three species of *Baltisphaeridium* were recorded. *B. longispinosum* (Eisenack 1931) is the commonest, ranging from the base of the Hope Shales to the top of the Caradocian and frequently occurring in large numbers (samples S21, C14/b). Populations of *B. longispinosum* show great morphological variation and consist of the forms *latiradiata* Eisenack 1959b and *filifera* Eisenack 1959b, and specimens transitional to *B. robustum*

(Sannemann 1955) and to *B. hirsutoides* (Eisenack 1939 emend. Eisenack 1951). Typical *B. robustum* and *B. hirsutoides* were not found. Rarely, however, forms attributable to *B. hirsutoides* but transitional to *B. longispinosum* were found in upper Caradocian sediments. Specimens attributable to *B. polygonale* (Eisenack 1931) were found in the lower Llanvirnian and upper Caradocian. In contrast with the Baltic specimens (Eisenack 1959b) the spine tips appear to contain no dark material.

2. *Veryhachium* Deunff (1954) 1958 emend. Downie and Sarjeant 1963.

Two species of *Veryhachium* have been found. *V. lairdi* (Deflandre 1946) Deunff 1954 from the Hope Shales was represented by specimens up to 150 μ in diameter (body diameter + process length). The largest specimens from Veryhac'h (Deunff 1958) are 100 μ in diameter, whilst those from the Upper Llandoveryan of Belgium (Stockmans and Willi re 1963) are considerably smaller. *Veryhachium* sp. ranges from the base of the Hope Shales to the top of the Caradocian. The body is rounded triangular in outline and, from its apices, three long blade-like processes extend radially. Variation is apparently limited to the shape of the processes, which may be short and wide or long and thin. This species differs from *V. ? macroceras* Deunff 1958 in always having three processes, each weakly constricted where it meets the central body.

3. *Leiofusa* Eisenack 1938.

Three species of *Leiofusa* were found. Numerous specimens closely resembling *Leiofusa tumida* Downie 1959 were found in the upper Caradocian. They are much larger (total length = 200–350 μ) than typical examples of *L. tumida* from the Wenlockian, and the spherical to subspherical central body makes up only one-fifth of the total length; to some extent, however, the difference in size between the Wenlockian and Caradocian specimens may be a reflection of the different techniques used in their preparation. All the Caradocian specimens are closely similar in shape and have a clear hyaline test wall texture. They may belong to a new species, but until whole populations can be examined they are designated *L. cf. tumida* Downie.

Many specimens resembling *Leiofusa filifera* Downie 1959 were found in the Hope Shales. They are larger (total length = 300–650 μ) than Wenlockian examples of *L. filifera* (total length = 30–350 μ), and have proportionately smaller and less sharply defined central bodies. These specimens possibly belong to a new species also, but whole populations have not been examined; for the present they are designated *L. cf. filifera* Downie. Transitional forms linking *L. cf. tumida* and *L. cf. filifera* were not encountered.

A single specimen of *Leiofusa navicula* Eisenack 1951, twice the size of the holotype (total length = 420 μ , diameter = 100 μ), was found in the upper Caradocian (sample C14/b). The type material is from the Vaginatenkalk of Estonia.

4. *Bacisphaeridium* Eisenack 1962b.

About thirty specimens belonging to a single species of *Bacisphaeridium* were found in sample C14/b (middle Marshbrookian, Caradocian). They are closely similar in shape, and vary only slightly in size. The body is circular in outline and 105–172 μ in diameter, the process is uniformly wide and 230–284 μ in length. A single specimen found in sample C6 (basal Actonian, Caradocian) is considerably smaller than any of the Marshbrookian examples (body diameter = 70 μ , process length = 225 μ). No examples were found having two or more processes. The British species has a much longer process

(60–75 per cent. total length) than *B. bacifer* (Eisenack 1934) from the Wesenberg Beds of Estonia. *Demffia monacantha* (Deunff 1958) Downie 1960 has an oval-shaped body and a tapering process, and is one-third to half as large as the British specimens.

5. *Leiosphaeridia* Eisenack 1958a emend. Downie and Sarjeant 1963.

Leiospheres of various sizes were encountered, frequently in abundance, throughout the Ordovician successions of the Shelve and Caradoc districts, but no attempt has been made to classify them. Some specimens compare closely with *Leiosphaeridia voighti* Eisenack 1958 in the size and the thickness of their test walls. A number of tests folded into a fusiform shape like *Leiosphaeridia* cf. *baltica* Eisenack 1958a (pl. 2, fig. 12), but much larger, were found in a few Llandeilian and Caradocian assemblages. These are attributed to *Leiosphaeridia* for the present, but their frequent occurrence in clusters, each specimen apparently folded in exactly the same manner, makes the propriety of this identification doubtful.

In order to ascertain the prospects for future research on the Ordovician acritarchs of Shropshire, the fine-fractions of several residues (i.e. the portions of the residues passing the 300-mesh sieve) were mounted for examination under the microscope. In the Shelve samples the preservation of acritarchs is generally poor. The fine-fractions of the residues from samples S21 (basal Hope Shales), S1 (Weston Beds), S11 (Meadowtown Beds) contained a variety of forms including species of *Baltisphaeridium*, *Michrystidium* Deflandre 1937 emend. Downie and Sarjeant 1963, *Veryhachium*, and *Leiofusa*. The actual numbers of specimens, however, were generally small, and only a small proportion of them were identifiable. The large numbers of fragmentary specimens in the Shelve assemblages suggests that quantitative studies will not generally be possible.

Well-preserved acritarchs are common in samples from the Caradoc area. The fine-fractions of the residues from samples C11 (lower Caradocian), C9 (middle Caradocian), C14/b, and C1/a (upper Caradocian) contained a variety of forms belonging to *Baltisphaeridium*, *Michrystidium*, *Veryhachium*, *Leiosphaeridia*, and *Leiofusa*. Large numbers of well-preserved, identifiable specimens were found, and it appears that quantitative studies will generally be possible.

It is noteworthy that representatives of *Tasmanites* Newton 1875 (Chlorophyceae) were not found during the present study.

? *Fungi*. The existence of unidentified boring organisms (? fungi) is suggested by the occurrence of holes in the tests of some chitinozoans (Pl. 72, figs. 8–9). These hypothetical organisms appear to have been active before fossilization took place and to have affected only certain species, in particular *Cyathochitina knickersiana* (q.v., p. 459). Evidence for their existence, in Britain, has been found only in sediments from the Caradoc area, while no actual remains of the organisms themselves have been seen.

Foraminifera. In carefully prepared residues, the organic linings of Foraminifera may be found more or less complete. They break up readily and the organic residues of some samples contain large quantities of fragmented linings.

STRATIGRAPHICAL DISTRIBUTION OF CHITINOZOANS IN SHROPSHIRE

The average stratigraphical interval between samples is about 170 ft. At several localities, however, a number of samples were collected at intervals of a few feet in

order to determine the extent to which the character of the chitinozoan fauna was varying within short vertical intervals. After examining several sets of these adjacent samples it appears that within short sequences of either mixed or uniform lithology, the concentration of chitinozoans in the sediment may vary greatly and capriciously, but the relative abundance of each species (i.e. number of examples per thousand chitinozoans) remains much the same, and the same species are present.

A very common and perhaps universal character of chitinozoan assemblages is the relatively small number of species they contain. The average number of species in each of thirty-one assemblages from Shropshire is seven, the least varied assemblages consisting of only two species, the most varied consisting of twelve to fourteen species and up to nine other forms. The chitinozoans from the Shropshire assemblages belong to thirteen genera, one of them new, and have been allocated to thirty-two species, nineteen of which are new. A considerable number of forms occurring in these assemblages have not been described in this paper; in general they are neither referable to previously named species, nor are they adequate bases for the establishment of new species.

The previously named species found in Shropshire appear to be characteristic Ordovician forms. None of them has been recorded in the Devonian of the New World, North Africa, or Europe, nor in the Silurian of the Baltic. The few reported from the Silurian of the Sahara require special mention. *Lagenochitina cylindrica* Eisenack (undescribed and unillustrated by Taugourdeau and Jekhowsky (1960)) was recorded in a single Middle Silurian sample where it was very rare; *Conochitina elegans* (recorded as *Rhabdochitina conocephala* by Taugourdeau and Jekhowsky (1960)) was found in a single Lower Silurian sample; and rare specimens of *Cyathochitina campanulaeformis* (unillustrated and described as being somewhat different from typical forms by Taugourdeau (1962)) occurred in one or more Llandoveryan samples. *Rhabdochitina magna* has been recorded in two Lower Silurian samples by Taugourdeau and Jekhowsky (1960) who, I believe, interpret this species more widely than would be justifiable on the basis of the Baltic and British material. Cramer's (1964) reports of *Conochitina elegans* (designated *Rhabdochitina conocephala*) and *Cyathochitina campanulaeformis* from the Silurian of Spain are probably based upon misidentified material; the specimens Cramer figures as examples of these two species clearly do not support his identifications.

Distribution in the Llanvirnian. Except for some examples of *Sphaerolithina vulgaris* bearing very small spines and cones, chitinozoans from the Llanvirnian of Shropshire have perfectly smooth test walls. Several species, including *Conochitina chydaea*, *Cyathochitina campanulaeformis*, *Rhabdochitina usitata*, *R. turgida*, and *Siphonochitina robusta* range through the whole of the Llanvirnian but are not restricted to it, whilst others have more limited ranges and may prove useful in subdividing the series. Assemblages from the lower Llanvirnian (Hope Shales) are strikingly characterized by species of *Siphonochitina* having slender tests and large siphons (*S. formosa* and *S. tenuicollis*); nothing comparable with them has been found elsewhere and they may prove to be useful stratigraphical markers, at least locally. With them, and sometimes in large numbers, occur *Siphonochitina robusta* and *Conochitina parviventer*, but the latter do occur elsewhere, though infrequently and only in reduced numbers. *Cyathochitina calix*, *Lagenochitina cylindrica*, and *L. esthonica* have been found only in the basal Hope Shales.

Only two new forms (*Pterochitina* sp. and *Siphonochitina clavata*) appeared in the middle and upper Llanvirnian (Stapeley Shales, Weston Beds, Betton Beds) to take the place of the missing lower Llanvirnian forms. *Pterochitina* sp. was found at the top of the Stapeley Shales whilst *S. clavata* was first recorded in the Betton Beds and extends into the lower Caradocian. It is remarkable that *Desmochitina minor* was not found in British Llanvirnian sediments, since it occurs in considerable numbers at this time in the Baltic.

Distribution in the Llandeilian. Llandeilian assemblages differ from those of the Llanvirnian in that species of *Siphonochitina* are absent and *Desmochitina minor* is present. There are otherwise no marked differences between upper Llanvirnian and Llandeilian assemblages, the latter being comprised almost entirely of forms continuing from the Llanvirnian. With the exception of some examples of *Conochitina chydaea* which bear an ornament of small cones, Llandeilian chitinozoans, like those of the Llanvirnian, have smooth test walls. *Desmochitina minor* was found throughout the series, where its shape is quite distinct and somewhat different from that of *D. minor* forma *typica* and forma *cocca* of the Caradocian. Llandeilian chitinozoans from Shropshire are morphologically simple, lacking elaborate ornamental and structural elements; and numerically large assemblages contain very few species. These do not appear capable of supporting any subdivision of the series.

Distribution in the Caradocian. The chitinozoan assemblages of the Llandeilian and Caradocian are quite distinct and separated by an abrupt faunal change. Caradocian assemblages are characterized by forms with wide skirt-like carinae, appendices of various types and, in the upper part, several distinct styles of ornamentation; in addition, fifteen species and five genera appear for the first time in this series.

Conochitina elegans, *Cyathochitina kuckersiana*, *Desmochitina minor* forma *typica*, and *Lagenochitina baltica* first appear at the base of the Caradocian and persist throughout the series. Whilst they play no part in subdividing the series these forms readily distinguish Caradocian from earlier assemblages. In Britain, it is not known whether these four forms continue above the Caradocian, but in the Baltic, where younger sediments have been studied, *C. elegans* has been found only in the lower part of the Caradocian (C₂-D₂), *L. baltica* only in the Ashgillian (F₁), and *C. kuckersiana* and *D. minor* f. *typica* in both the Caradocian and Ashgillian (C₂-F₁). None of these four forms has been recorded from the Baltic Silurian.

The lowest Caradocian strata are distinctive because *Ancyrochitina* is absent. It first appears at the base of the Glenburrell Beds but with the main generic character, the appendices, weakly developed (*A. bulmani*). Typical forms of *Ancyrochitina* first occur about half-way through the Caradocian (*A. alaticornis*), at roughly the same time as the earliest Baltic record (*A. multiradiata* in D₁, Eisenack 1959a). *A. alaticornis* ranges from the Alternata Limestone through the Cheney Longville Flags and into the basal Acton Scott Beds, where it is accompanied, in abundance, by *Hoegisphaera complanata* and *Sphaerochitina actonica*, neither of which has been found elsewhere in Britain.

Near the top of the Caradocian, a pronounced and fairly abrupt change takes place in the chitinozoan fauna. Earlier assemblages, consisting very largely of forms with smooth test walls, give way to assemblages containing forms with strongly developed

LLAN-VIRNIAN	LLAN-DEILIAN	CARADOCIAN	
S2 S1 S37 S36 S21 S25	S8 S5 S4 S3 S11	C1f-h C1e C1d C1a-c C2d C2c C2b C2a C4 C6 C14b C8/b-c C9 C11 C16	Sample Species
+		+	<i>Sphaerochitina actonica</i> <i>S. vulgaris</i>
++ +		+ +	<i>Siphonochitina robusta</i> <i>S. clavata</i>
++ +		+	<i>S. cf. pellucida</i> <i>S. tenuicollis</i> <i>S. formosa</i>
+++ ++ +	++ +	+ ++++	<i>Rhabdochitina usitata</i> <i>R. turgida</i> <i>R. magna</i>
+		+ +	<i>Pterochitina</i> sp. <i>Lagenochitina capax</i> <i>L. shelvensis</i>
++ +		+++ + ++ +	<i>L. esthonica</i> <i>L. cylindrica</i> <i>L. baltica</i>
		+ ++ +	<i>Hoegisphaera complanata</i> <i>Hercochitina downiei</i> <i>D. minor</i> f. <i>cocca</i>
	+ ++	+++ +++ ++++	<i>D. minor</i> f. <i>typica</i> <i>Desmochitina minor</i> s.l. <i>Cyathochitina kuckersiana</i>
++ +	+++	+++ ++++ ++++	<i>C. campanulaeformis</i> <i>C. calix</i> <i>Conochitina elegans</i>
++ ++++	+ ++++	++ +	<i>C. parviventris</i> <i>C. chydrea</i> <i>C. lepida</i>
		++ ++++ +	<i>Angochitina dicranum</i> <i>A. communis</i> <i>Ancyrochitina bulmani</i>
		++++ ++++ ++++	<i>A. alaticornis</i> <i>A. omiensis</i> <i>Acanthochitina barbata</i>

Table I. Vertical distribution of some species of chitinozoans in the Ordovician of Shropshire

and very varied ornamental processes. Within a stratigraphical interval of 50 ft., five strongly ornamented species (*Acanthochitina barbata*, *Ancyrochitina onniensis*, *Angochitina communis*, *A. dicranum*, and *Hercochitina downiei*), and three genera (*Acanthochitina*, *Angochitina*, and *Hercochitina*) whose chief diagnostic features are their ornamentation, appear for the first time in Britain. Whilst *Angochitina dicranum* and *Hercochitina downiei* appear to be very short lived and may prove useful in local correlation, *Acanthochitina barbata*, *Ancyrochitina onniensis*, and *Angochitina communis* continue to the top of the succession.

Four types of chitinozoan assemblage have been distinguished in the Caradocian of Shropshire.

Assemblage type 1. The oldest Caradocian assemblages are characterized by the four typical Caradocian forms (*Conochitina elegans*, *Cyathochitina kuckersiana*, *Desmochitina minor forma typica*, and *Lagenochitina ballica*) and the absence of species of *Ancyrochitina*. This type of assemblage occurs at the base of the Caradocian, extending into the Harnagian but no higher than the base of the Glenburrell Beds.

Assemblage type 2. The stratigraphical range of this type of assemblage is known only approximately, extending certainly from the middle Harnagian and possibly from the lower Harnagian to a level somewhere below the Alternata Limestone. Chitinozoans characteristic of this type of assemblage are *Ancyrochitina bulhuani*, which has remarkably small and sometimes numerous appendices, and *Desmochitina minor forma cocca*.

Assemblage type 3. The most important feature of this type of assemblage is the presence of *Ancyrochitina alaticornis*, readily distinguished by its spectacular wing-like appendices, which commonly bear secondary processes on the thinner edge. The vertical range of this type of assemblage embraces the Alternata Limestone, the Cheney Longville Flags, and the basal Acton Scott Beds; it possibly includes older strata but it does not reach the top of the Acton Scott Beds. *Hoegisphaera complanata* and *Sphaerochitina actonica* are abundant in the basal Acton Scott Beds and may prove useful in dividing this assemblage type further.

Assemblage types 3 and 4 are separated by about 250 ft. of beds in which neither *Ancyrochitina alaticornis* nor the diagnostic chitinozoans of assemblage type 4 have been found.

Assemblage type 4. This type of assemblage is distinctive because of the variety and abundance of forms with ornamental processes. It is strikingly different from the assemblages found at lower horizons, in which forms with smooth test walls predominate. Characteristic species are *Acanthochitina barbata*, which is furnished with uniformly distributed short pillars supporting a raised reticulum, and *Ancyrochitina onniensis* and *Angochitina communis*, both of which bear simple and wishbone spines. Assemblages of this type occur only in the top 70–80 ft. of the series (upper Onnia Beds). Two distinctive species with known vertical ranges of about 15 ft. characterize the earliest assemblages of this type. They are *Angochitina dicranum*, which has pitchfork-shaped spines, and *Hercochitina downiei*, the spines of which are arranged in longitudinal rows and connected at their tips by longitudinal bars running parallel with the test wall.

COMPARISON WITH ORDOVICIAN FAUNAS FROM THE
BALIC AND NORTH AFRICA

In many respects the chitinozoan faunas of the Baltic and British Ordovician are closely comparable. Communication between them appears to have been generally fairly free and apparently at its maximum during the Caradocian. Eleven species found in Shropshire (*Acanthochitina barbata*, *Conochitina elegans*, *Cyathochitina calix*, *C. campanulaeformis*, *C. knickersiana*, *Desmochitina minor*, *Hoegisphaera complanata*, *Lagenochitina baltica*, *L. cylindrica*, *L. esthonica*, and *Rhabdochitina magna*) have been described by Eisenack from the Baltic, where they appear to be characteristic Ordovician forms.

In Llanvirnian times, communication between the Baltic and British faunas appears to have been less free than it was during the remainder of the Ordovician. The most striking differences between the two faunas at this time are, firstly, the abundance and variety of *Siphonochitina* in Britain and its apparent absence in the Baltic, and secondly, the absence of *Desmochitina* in British assemblages; this distribution suggests that some factor, perhaps an ecological difference, was hindering the spread of certain forms between the two regions. However, in spite of this hypothetical factor five of fourteen British Llanvirnian species (*Cyathochitina calix*, *C. campanulaeformis*, *Lagenochitina cylindrica*, *L. esthonica*, and *Rhabdochitina magna*) occurred in the Baltic, all but *L. cylindrica* (horizon unspecified) during some part of the Llanvirnian.

It appears that the generic differences between the two North European Llanvirnian faunas did not persist into the Llandeilian. In both regions at this time, species of *Siphonochitina* were apparently absent and *Desmochitina* was represented by *D. minor*. However, the conservative morphology of *D. minor* throughout the British Llandeilian contrasts with the variety it assumes in the Baltic. Three of seven British Llandeilian species (*Cyathochitina campanulaeformis*, *Desmochitina minor*, and *Rhabdochitina magna*) have also been found in the Baltic at this time. These facts suggest that communication between the two faunas in Llandeilian times was, to some extent, more free than in the Llanvirnian.

The Caradocian faunas of Shropshire and the Baltic correspond closely. In both regions *Cyathochitina knickersiana* and *Desmochitina minor* f. *typica* occur throughout the series, and typical examples of *Ancyrochitina* first appear at approximately the same stratigraphical level. *Conochitina elegans*, which has been found throughout the series in Britain, ranges through at least the lower half of the Baltic Caradocian (C₂-D₂). A variety of cylindroconical forms having simple, generally short, spines occurs in the majority of British Caradocian assemblages. These forms are not described in this paper but they possibly represent *Conochitina micracantha* Eisenack 1931 of the Baltic; further work is necessary to determine which, if any, of Eisenack's several forms of this species are represented in Britain.

Besides these similarities, however, there are several striking differences between the two Caradocian faunas. In Britain, *Cyathochitina campanulaeformis* is last found in the Llandeilian, whilst in the Baltic it continues through the Caradocian and into the Ashgillian. *Lagenochitina baltica* is characteristic of assemblages from the base and summit of the British Caradocian, but in the Baltic it occurs in the *Diplograptus*-Kalk, and in the Lyckholm Beds which are considered to be Ashgillian. The difference between

the two faunas is emphasized by the lack of variety and scarcity of *Ancyrochitina* in the Baltic, and by the absence of *Parachitina* and *Conochitina mimmesotensis* Stauffer 1933 in Shropshire. The appearance of *Acanthochitina barbata* and the genus *Angochitina* at the top of the British Caradocian slightly anticipates their appearance in the Lyckholm Beds of the Baltic, suggesting that the dispersal of chitinozoans was sometimes fairly slow, or that the *Omnia* Beds are only slightly older than the Lyckholm Beds.

Eisenack (1962a) outlined the stratigraphical occurrence, in the Baltic, of three apparently closely related species of *Cyathochitina* (*C. calix*, *C. campanulaeformis*, *C. kuckersiana*). *C. calix* ranges from B₂ (Arenig) to C₁ (upper Llanvirnian–Llandeilian) and is then replaced by *C. campanulaeformis*. *C. kuckersiana* develops from *C. campanulaeformis* in the lowest Caradocian, C₂, and both species continue through the Caradocian into the Ashgillian, F₁. These three species also occur in Shropshire. However, *C. calix* has been found only at the base of the Llanvirnian, where it is accompanied by typical examples of *C. campanulaeformis* and a few forms transitional between the two species. *C. campanulaeformis* ranges from the base of the Llanvirnian into the Llandeilian but was not found in the Caradocian. As in the Baltic, *C. kuckersiana* first appears at the base of the Caradocian and continues to the top of the series, but the species is generally represented by forms closer to forma *brevis* than to typical *C. kuckersiana*; in the Baltic, f. *brevis* is found from D₁ to D₃ (middle Caradocian). Since these three species are so similar their identification is possibly somewhat subjective. However, I have attempted to distinguish them in precisely the same manner as their author (Eisenack), and have discussed with him, in correspondence, the differences between *C. campanulaeformis* and *C. kuckersiana*.

The Ordovician chitinozoan faunas described by Taugourdeau and Jekhowsky (1960), and Benoit and Taugourdeau (1961) from North Africa compare only remotely with the British fauna and include only two of the species (*Rhabdochitina magna* and *Siphonochitina pellucida*) recognized in Shropshire. It should be noted, however, that three species known from the Ordovician of Britain and the Baltic (*Cyathochitina campanulaeformis*, *Lagenochitina baltica*, *L. cylindrica*) have been included in a chart (Benoit and Taugourdeau 1961) showing the ranges of some North African Ordovician chitinozoans, but that none of them has been described or figured. The fact that *Clathrochitina* is represented in several North African Ordovician assemblages but has not been found in Shropshire emphasizes the differences between the two faunas. On the other hand, however, it is remarkable that chitinozoans belonging to the genus *Siphonochitina* occur in Ordovician assemblages from North Africa (Benoit and Taugourdeau 1961, Combaz and Poumot 1962) and Britain, but are unknown in the Baltic.

From the information presently available, it appears that communication between the Ordovician faunas of Shropshire and the Baltic was fairly free, especially in Caradocian times, whilst communication between the North European and North African faunas was considerably more limited.

Chitinozoan assemblages have also been found in the Ordovician Rhenish Schiefergebirge (Eisenack 1939), the Llanvirnian–Llandeilian of Bohemia (Eisenack 1948), the Middle Ordovician Tulip Creek Formation of Oklahoma (Wilson and Dolly 1964), the Upper Ordovician Sylvan Shale Formation of Oklahoma (Wilson 1958) and the Caradocian Nod Glas Formation of Merioneth (Rhodes 1961). These assemblages are Ordovician in character but too little is known about them to allow adequate

comparison with the chitinozoan faunas from the Baltic, Shropshire, and North Africa.

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SPINATRYPA AND SPINATRYPINA (DEVONIAN BRACHIOPODA)

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ABSTRACT. The Eifelian–Givetian (Middle Devonian) sediments of Germany contain a near-continuous suite of brachiopods belonging to the genera *Spinatrypa* Stainbrook 1951 and *Spinatrypina* Rzhonsnitskaya 1964. These two allopatric atrypid genera occupy different, mutually exclusive environments: the first is dominant in a brachiopod biotope, and the other is invariably associated with small thamnoporid or disphyllid corals. Several new taxa of limited vertical distribution are briefly described. These are *Spinatrypa variaspina*, *S. aspera meridiana*, *S. globulina*, *S. curvirostra*, *S. orthoclina*, and *Spinatrypina demissa*, *S. fabaca*, *S. girzenensis*. Small changes in critical correlations of the Eifel region are suggested. In Germany, and probably elsewhere in Europe, the *Spinatrypa*–*Spinatrypina* atrypids of Givetian age predominantly replaced the *Atrypa* group common to Eifelian rocks, a feature possibly of major significance in marking the Eifelian–Givetian boundary.

A MAJOR part of the Middle Devonian atrypid faunal record consists of species belonging to two genera, *Spinatrypa* and *Spinatrypina*. On the basis of slightly less than 10,000 specimens, mainly from the Devonian synclines of the Eifel region, but also from Bergisches Land east of the Rhine (Germany), fifteen species and subspecies are described, most of them in abridged form and many for the first time. Since these atrypid taxa have a short vertical range, they are especially useful in more detailed Eifelian–Givetian correlations of north-western Europe.

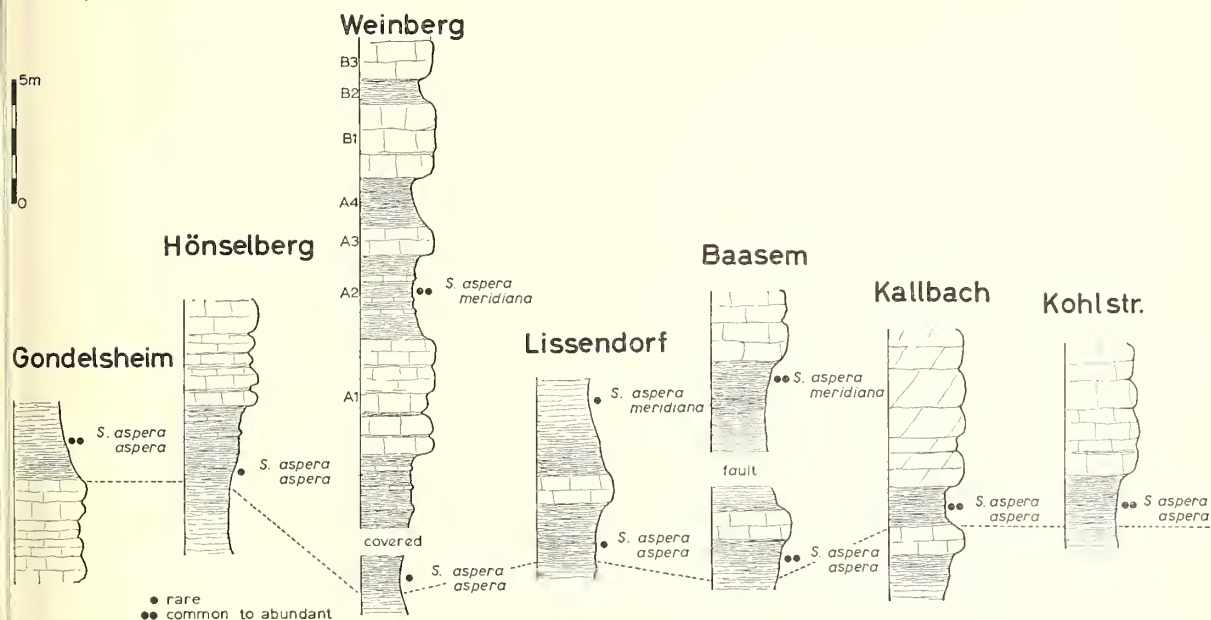
Type and figured specimens are housed for the greater part in the British Museum (Natural History). The remaining collections belong to the author, but substantial portions used in the revisions were also on loan from the Natur-Museum Senckenberg (Frankfurt am Main, Germany) and the Paläontologisches Institut und Museum (Humboldt-Universität, Berlin, Germany). A fine collection from the Paffrath syncline was donated by Dr. Ulrich Jux (Universität Köln, Germany). British Museum specimens are catalogued under the code number BB. Under ‘Material’ for each specific description, the numbers of specimens collected are cited. Details of grid references reach excessive length and are left for future record. Material was derived from some 600 fossil localities. Where given (e.g. under Stratigraphy and text-figures), the grid references follow the standard German five-digit controls based on the kilometre scale.

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STRATIGRAPHY

The geological sequence in the Hillesheim syncline has become generally accepted by Eifel workers as the type Middle Devonian succession for the Eifel region (text-fig. 1). In this syncline, the Eifelian and Givetian rocks reach a thickness of about 750 m. and from the base to the top are marked by a gradual, much interrupted transition from a brackish water, littoral environment to a fully marine environment rich in brachiopods,

along the Giesdorf and Eilenberg horizons. The problem has plagued Eifel stratigraphers for several years and is still not wholly solved. Fossils are abundant, but the faunal content of one locality frequently varies strikingly from the next. In the Prüm syncline, the Giesdorf horizon is marked by the conspicuous spiriferid *Spinocyrtia ostiolata* and this horizon has been suitably taken as the top of the Junkerberg beds. Unfortunately, *Spinocyrtia* has a localized distribution and is not common outside the Prüm syncline (viz. Metje 1956, Ochs and Wolfart 1961, Struve 1961). Directly above the *ostiolata*



TEXT-FIG. 2. Critical stratigraphic successions with *Spinatrypa aspera* (Schlotheim) in the Eifel region, Germany. Thicknesses estimated or measured. Grid references—Gondelsheim, MTB Gerolstein r36880 : h65910; Hönselberg, MTB Dollendorf r53850 : h74680; Weinberg, MTB Dollendorf r50980 : h75720; Lissendorf, MTB Stadtkyll r42280 : h75680; Baasem, MTB Hallschlag r35150 : h81110; Kallbach, MTB Mechernich r38020 : h96980; Kohlstr., MTB Mechernich r37910 : h96450.

horizon on the north flank of the Prüm syncline, specimens of *Spinatrypa aspera aspera*, sensu restricto, are common.

Spinatrypa aspera (Schlotheim), an index fossil of the Freilingen beds (upper Eifelian) was re-examined. It was found that two different variations, here classed as subspecies, were identifiable, even under the restricted usage of the Schlotheim atrypid in Struve (1956, 1961, 1964). It was also noted that the *Spinatrypa aspera aspera* of Struve (1961, p. 313) was in fact different from the topotypical *S. aspera*, and could be called a new type *S. aspera meridiana*. In two stratigraphic sections (text-fig. 2), this new and different type of *aspera* was found stratigraphically above the topotypical *aspera*.

Struve (1961, p. 310) has assumed that the lower part of the Freilingen sequence does not contain *Spinatrypa aspera aspera*, probably because it has not been found with the typical Eilenberg horizon fauna of *Kerpina vineta* Struve. This absence can, however, probably be accounted for by the peculiar biotope complex of the Eilenberg horizon.

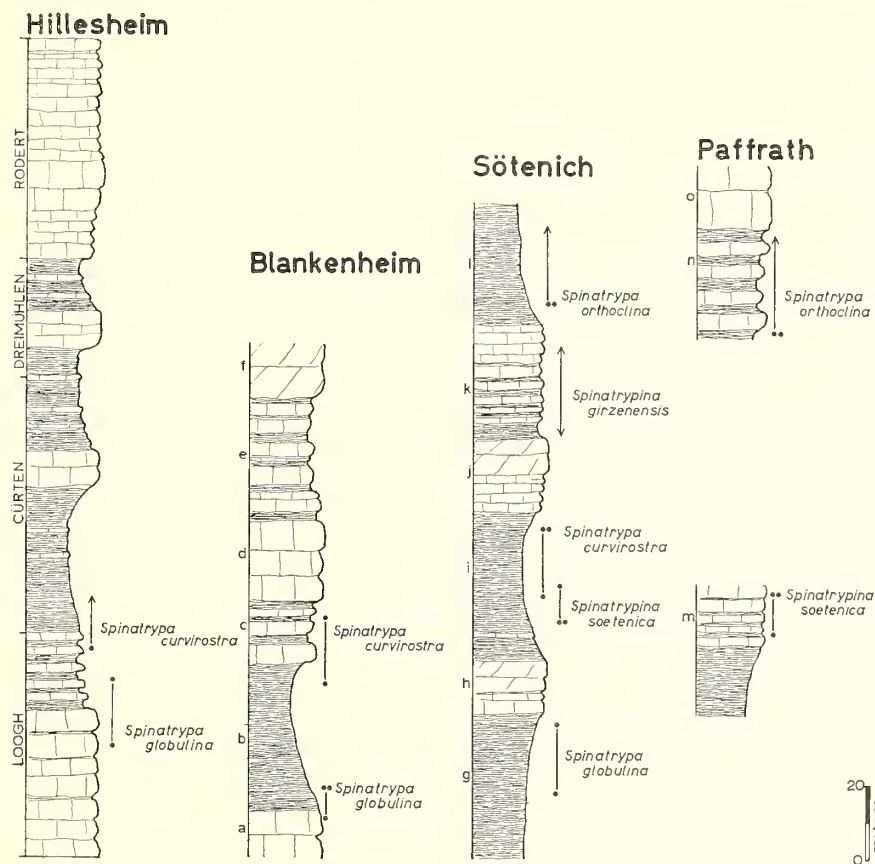
Since Struve concluded that the lower Freilingen beds lacked *aspera*, it was necessary to suppose that there must have been marked stratigraphic hiatuses in the lower Freilingen beds of the Prüm syncline, because here *aspera* lies directly above the top of the Junkerberg beds. As support for such hiatuses Struve (1964, p. 239) cited the presence of an ironstone bed at nearly the same position, and which, it was alleged, 'ist eine typische Transgressions-Bildung'. However, this ironstone bed is not well marked and usually not noticeable in field localities. Other evidence of a sedimentological break (e.g. re-worked sediment, shelly debris, mud cracks, ripple marks) is apparently absent. Moreover, there is good evidence that *Spinatrypa* is often strongly indicative of quieter, possibly deeper water (Copper, in press). Proof of a Prüm hiatus is weak.

At the type and neighbouring localities of *Spinatrypa aspera aspera*, s.r., in the Sötenich syncline, the fossiliferous beds are overlain by sterile limestones or dolomites. At two other localities (Baasem in the Blankenheim syncline, Lissendorf in the Dollendorf syncline), the subspecies *aspera* is followed by *meridiana* n.ssp. in well-exposed sections. Predictably then *aspera* should also be found below *meridiana* in the Hillesheim syncline. At present this occurrence can be confirmed at Hönselberg and outside the Weinberg quarry (text-fig. 2), though not in outcrop and certainly rare. It seems likely that *Spinatrypa aspera aspera* occurs in stratigraphic equivalents of the Eilenberg horizon and perhaps even below it, though not in the Junkerberg beds. A change in the definition of the Freilingen beds, previously divided into an upper unit with *S. aspera aspera* and a lower unit without it (Struve 1961, p. 310), seems required. It also means that the type stratum of the topotypic material of *Spinatrypa aspera aspera* becomes more or less coeval with the Eilenberg horizon, thereby eliminating the need to postulate hiatuses in the Prüm syncline.

Strong corroboration for this new interpretation was found in the stratigraphic position of two other atrypid species, still undescribed but in part probably predicted by Krömmelbein (1953, pp. 66, 67) as 'eine bezeichnende *Atrypa*-Art'.

Another critical correlation sequence to which the *Spinatrypa* group makes a contribution is the lower and middle Givetian column of the northern synclines in the Eifel region (text-fig. 3). During this period, the fossiliferous atrypid beds are almost wholly confined to the northern synclines while the southern synclines contain sparse, possibly dwarfed atrypid faunas which are difficult to compare. Correlations on a horizon-by-horizon basis are complicated. The last rich Givetian atrypid fauna of the south (with the exception of the puzzling 'Mühlwäldchen' material) is in the Rech horizon with its *Spinatrypina wotanica* (Struve). The Wachtberg horizon of the Sötenich syncline (Schmidt and Schröder 1962) and the Neuenbüsch horizon of the Blankenheim syncline (Ochs and Wolfart 1961) are probably roughly coeval and can be correlated with the middle Wotan to middle Rech horizons of the Hillesheim sequence (refer to text-fig. 1). The age of the Spickberg dolomites is tentatively placed as upper Loogh. The Scheid horizon with *Spinatrypa curvirostra* n.sp. can be dated as upper Rech to Felschbach in age. In 1962 Jux confirmed the Scheid horizon with this same species as middle Eifelian in age, though this was corrected later (Jux 1965, p. 159). *Spinatrypina soetenica* (Struve) is still uncertainly dated, but is probably restricted to the Felschbach horizon. *S. girzenensis* n.sp. from the thamnoporid coral rich beds south of Keldenich in the Sötenich syncline is certainly younger than the Scheid horizon, but probably not of Rodert age: it is dated as Dreimühlen.

Paulus (1959, p. 359) and Schmidt and Schröder (1962, p. 37) give the fossiliferous shales of Urfe valley a Kerpen age, mainly on the basis of trilobites. Indirectly, however, the brachiopod evidence suggests an older age. The Urfe beds carry a coral and brachiopod fauna with *Spinatrypa orthocline* n.sp. which is similar, if not identical, to the fauna of the Torringer beds in the Paffrath syncline outside the Eifel. Jux (1964,



TEXT-FIG. 3. Critical stratigraphic successions of the lower and middle Givetian in the Eifel region and Bergisches Land, Germany. Data compiled from Hotz *et al.* 1955, Ochs and Wolfart 1961, Schmidt and Schröder 1962, Jux 1964. Code: a—Pierensberg horizon, b—Neuenbüsch horizon, c—Buir horizon, d—Ermberg 'horizon', e—Kerpen beds, f—dolomite unit, g—Wachtberg horizon, h—Zilckens horizon, i—Scheid horizon, j—Spickberg beds, k—unnamed unit (herewith), l—Urfe beds, m—Odenthal quarry, n—Torringer beds, o—Büchel beds.

p. 164) has dated the Torringer beds as Rodert, and followed the interpretation of Hotz *et al.* (1955, p. 151). This correlation concurs with the atrypid evidence. Moreover, it seems possible that the upper part of the Urfe beds (locality 17 in Paulus 1959, p. 359) can be separated from the lower part (locality 16, *ibid.*) on the basis of differences in *S. orthocline* n.sp., here still regarded as infraspecific.

Near Odenthal in the Paffrath syncline (Bergisches Land), a small atrypid-rich sequence can be correlated with basal portions of the Felsbach horizon (or Scheid

horizon of the Sötenich syncline) on the presence of *Spinatrypa soetenica* (Struve). This correlation makes the Odenthal beds considerably older than given in Jux (1964) who placed the Odenthal strata level with the *quadrigemina* beds of Hand.

SYSTEMATIC DESCRIPTIONS

Order ATRYPIDA Rzhonsnitskaya 1960

Superfamily ATRYPACEA Gill 1871

Family ATRYPIDAE Gill 1871

At the present time very few developmental series have been established for the atrypid brachiopods and many postulated generic or specific links are weakened because of the lack of internal structure information. The true relationship between *Spinatrypa* and *Spinatrypina*, for example, is far from clear. The two genera obviously inhabited different environments, but whether their morphology is due to divergence from a single stock or to later convergence from an *Atrypa* ancestor, remains doubtful. Both genera appear to show a number of iterative clines during Devonian time (particularly of rib structure), but it does not appear justified at the moment to classify each cline as a separate taxon, e.g. of subgeneric status. The appearance and disappearance of such clines may be due to periods of widespread migration in Devonian history. It may also be debated if strong breeding barriers in palaeontological 'species' or stocks of Palaeozoic age really existed.

Size change may be a measure of phylogenetic development, though this characteristic must be tempered with ontogenetic and ecological observations. In *Spinatrypa* all the Eifelian species of north-western Europe, and from available published data also those of the Ural Mountains and the Kuznetsk basin (see Lyashenko 1959, Alekseeva 1962), were small, with a width rarely exceeding 20 mm. The first large *Spinatrypa* are found in Givetian rocks. Similarly, nearly all *Spinatrypina* of Eifelian age are small; larger size in this genus is not reached until much later in Givetian time. This factor may be useful in broad faunal comparisons, but it is not axiomatic that small size is indicative of Eifelian age.

Terminology is after Siehl (1962) and Struve (1955); internal structures are described according to techniques used in Copper (1965*a*, 1965*b*).

Genus *Spinatrypa* Stainbrook 1951

Type species. Atrypa aspera var. *occidentalis* Hall 1858, p. 515, pl. 6, figs. 3*a-d*.

Range. Wenlockian (Silurian) to Frasnian (Upper Devonian). *Spinatrypa infrequens* (Weller 1914, pp. 285-6, pl. 35, figs. 1-5) is reported as lower Carboniferous but may be Frasnian.

Distribution. World-wide.

Diagnosis. Biconvex through dorsibiconvex and planoconvex spinose atrypids with small interareas and small deltidial plates of primitive type, and ortho-hypercline beaks. Ribs are coarse, undulose-shallow, and raised at each growth lamella. Internally, thick pedicle layers are absent, fibrous and columnar layers limited. Deltidial plates minute, undeveloped, rarely hollow. Teeth bear dental nuclei or lateral cavities. Cardinal process

small, few-stranded, frequently amorphous. Crural bases round, thick; crura often feathered. Jugal plates straight, bulky, and relatively long.

Remarks. The original definition of the genus given in 1945 by Stainbrook is still largely valid. The name *Hystericina* which Stainbrook selected for this group of spinose atrypids was pre-occupied and replaced by *Spinatrypa* in 1951.

Spinatrypa is easily distinguishable superficially from the genus *Atrypa* Dalman 1828 by its undulose ribs arranged in interrupted rows: ribs are also coarser and shallower, growth lamellae more widely separated. Internally, *Spinatrypa* is even more dissimilar in lacking numerous interlayers of fibrous and columnar test, thick pedicle constrictions without differentiation into deltidial structures, and solid teeth of *Atrypa*. Jugal plates also are distinct: in *Atrypa* they are longer, bent, and more U-shaped and in *Spinatrypa* more irregular, smaller, and stubbier.

The diagnostic characters of *Invertrypa* Struve (1961, p. 334), which are a ventri-biconvex shell, small area, and loss of ribs but distinct mid-rib pair, are well developed only in one species, the type *Spinatrypa kelusiana* Struve 1956, and are hereby judged not to be of sufficient value to warrant separate generic status (viz. Biernat 1964, p. 315). There is also evidence that '*Invertrypa*' reverted to typical *Spinatrypa* in Givetian time, a feature difficult to explain in terms of normal zoosystematic taxonomy.

Spinatrypa differs from *Spinatrypina* Rzhonsnitskaya 1964 in its undulose, instead of tubular-imbricate ribs, in its minute area, and small deltidial plates, rather than relatively large area and plates, and in its development of spines which are prominent and abundant when preserved. *Spinatrypa* also reaches a far greater size and shows a more prominent anterior fold. *Spinatrypa* is chiefly sedentary as its size, beak structure, ribs, and convexity indicate, and inhabited a clayey, muddy base. *Spinatrypina* is an elevated, attached atrypid brachiopod confined to a thicket reef or Rasenriff type of environment with thamnopod or disphyllid corals.

Spinatrypa variaspina n.sp.

Plate 76, figs. 1–12

Name. Latin, *varius*, variable, changeable; *spina*, thorn, spine. Where observed, the spines are highly variable in direction.

Type locality. Road cut Lissingen-Büdesheim, MTB Gerolstein r44890:h64630 (locality C398). *Type stratum*, Schleit horizon or slightly higher, Nohn beds, Eifelian. *Source sediment.* Brownish green to dark brownish grey calcareous shales and thin limestone interbeds rich in fine bioclastic debris. *Associated fauna:* *Atrypa* sp., *Desquamatia ovata* Copper, *Grünewaldtia* sp.aff. *rhenana* (Priestersbach). Mainly brachiopods.

Diagnosis. Small, generally flattish, biconvex shells with a prominent protruding, ortho-cline beak, small but sharp-edged area. Specimens are somewhat roundish in outline but the hinge is well defined: there is a marked variation in dimensions from wider than long to longer than wide. Ribs are small, flat, spaced at nine to eleven per 10 mm. and terminate in disarrayed spines where these were observed. Growth lamellae spaced at about 1 mm. Fold weak.

Remarks. This species differs from *Spinatrypa dorsata* Biernat (1964, pp. 307–9) which is somewhat younger, in being more distinctly ribbed, in a much larger area and

prominent, orthocline beak, and in its flatter dimensions. *S. variaspina* is already more reminiscent of *S. aspera aspera* (Schlotheim 1813) but can be separated by finer, more delicate ribs and wider area as well as its shape.

Material. The species is scarce and makes up only a very minor fraction of the Nohn atrypid fauna at any locality. It is overshadowed by *Atrypa* and *Desquamatia* and appears to be more common on the southern and eastern fringes of the southern Eifel synclines. Total 103 specimens.

Spinatrypa cf. *dorsata* Biernat 1964

Plate 76, figs. 13–19

1964 *Spinatrypa dorsata* Biernat, pp. 307–9, pl. 3, figs. 1–8.

Remarks. Polish specimens of this species compare most closely with *Spinatrypa* found in the Bildstock horizon of the Ahrdorf beds in the Eifel. But the identification is still not positive. In the Bildstock horizon, *Spinatrypa* becomes abundant for the first time in the Eifel region, locally even outnumbering small *Atrypa*. Specimens of the Bildstock niveau are not wider than 15 mm., but somewhat higher up in the sequence (Niederehe horizon), the *Spinatrypa* become rare yet larger in size. The Eifel *S. dorsata* are small, rather rotund, somewhat longer than wide, and very flat-ribbed with prominent rib interruptions.

The serial sections figured by Biernat (1964, p. 309) are difficult to compare and sketchy. Biernat shows the delthyrial cavity plugged by solid calcite, a feature absent in Eifel specimens and not typical of *Spinatrypa* as a whole. Biernat also shows remarkable joined jugal plates not present in Eifel material sectioned (text-fig. 4). The Eifel specimen showed small deltidial plates, an elongated dental nucleus (but no cavity), short and stubby teeth, a prominent inner socket ridge, slightly feathered crura, a thick jugal plate, and spiralia with about ten whorls.

Material. Total about 250 specimens, some not yet catalogued. This species is particularly common in the Ahrdorf and Hillesheim synclines.

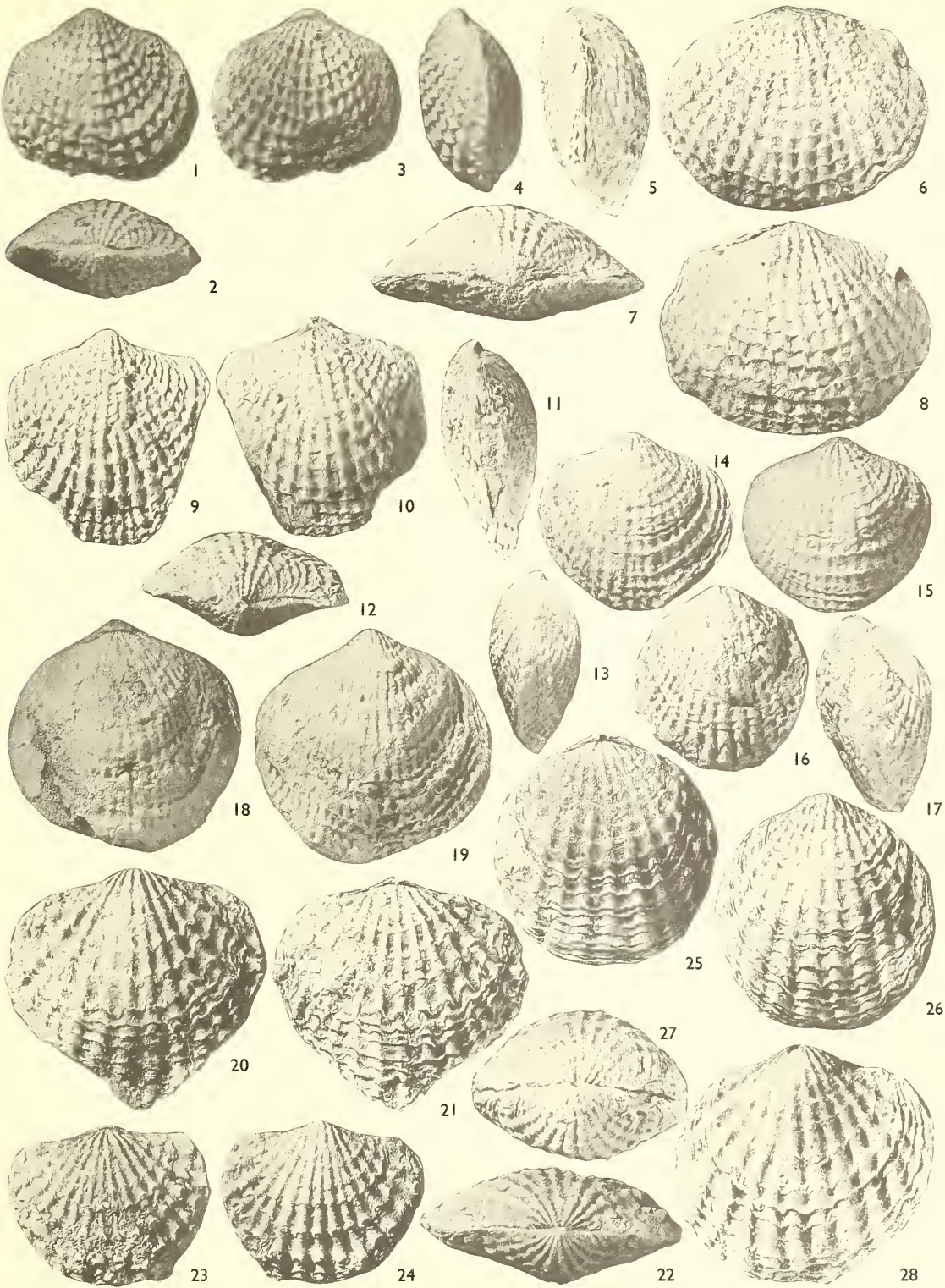
EXPLANATION OF PLATE 76

Figs. 1–12. *Spinatrypa variaspina* n.sp. Lower Eifelian, Weilersbach–Schleit horizons. 1–4, MTB Gerolstein r44890:h64630 (C398); 5–12, MTB Dollendorf r57000:h78230 (H252). 1–4, holotype BB55145, a small, slightly deformed specimen; 5–8, paratype PC62, wide coarsely ribbed shell with damaged umbo; 9–12, paratype PC63, elongate shell with prominent area.

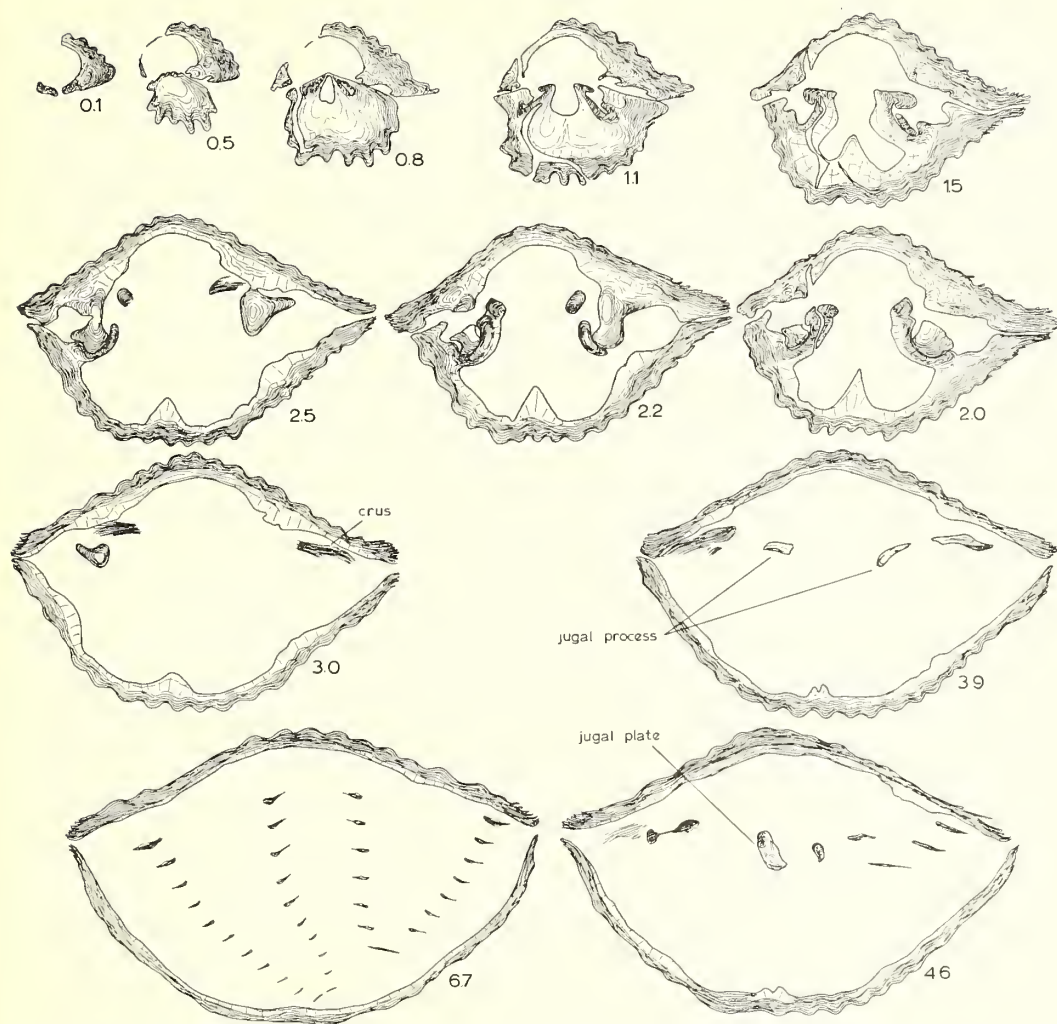
Figs. 13–19. *Spinatrypa* cf. *dorsata* Biernat 1964. Middle Eifelian. 13–17, Bildstock horizon; 18–19, Flesten–Niederehe horizon. 13–17, MTB Dollendorf r56340:h83560 (C252); 18–19, r55790–61100:h78000–90 (C249). 13–15, hypotype BB55150, typical small shell; 16–17, hypotype BB55149, more coarsely ribbed specimen; 18–19, hypotype BB55148, larger variety more common to higher horizons.

Figs. 20–28. *Spinatrypa aspera aspera* (Schlotheim 1813). Upper Eifelian, base of the Freilingen beds. 20–27, MTB Mechernich r37910:h96450 (C475); 28, MTB Mechernich r38020:h96980 (C468). 20–22, hypotype BB55153, large, straight, and wide-hinged variety; 23–24, hypotype BB55152, smaller, wide variety; 25–27, hypotype BB55155, normal elongate shell; 28, hypotype BB55151, large coarsely ribbed shell reminding of *S. semiorbis latecostata* Havlíček 1956.

All figures $\times 2$.



COPPER, *Spinatrypa* from the German Devonian



TEXT-FIG. 4. Transverse serial sections of *Spinatrypa* cf. *dorsata* Biernat 1964. The brachial umbo of this specimen is fractured. Bildstock horizon, lower Eifelian; MTB Dollendorf r54800 : h79180. Hypotype BB55223. $\times 4$.

Spinatrypa aspera aspera (Schlotheim 1813)

Plate 76, figs. 20–28; Plate 77, figs. 1–9

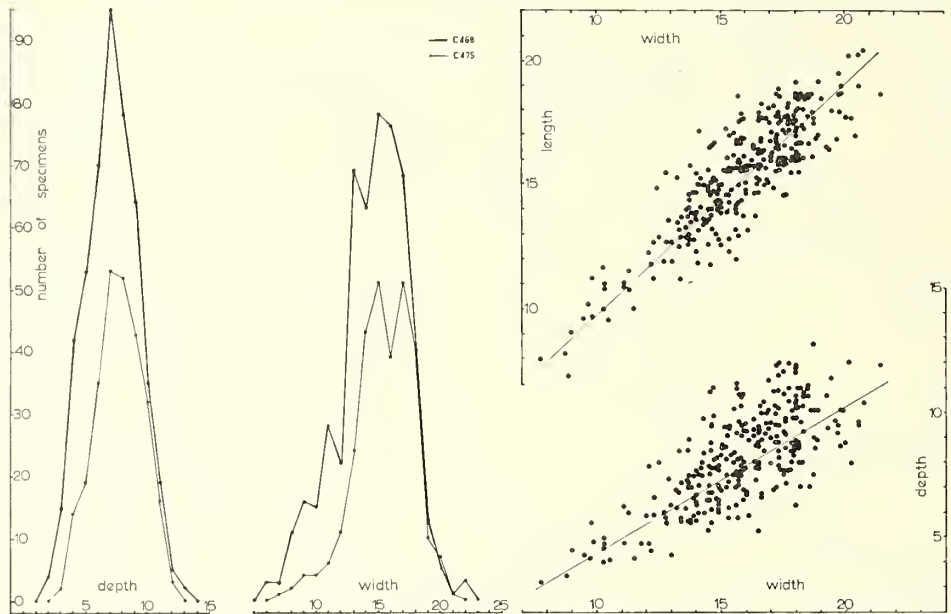
- 1813 *Anom. Terebratulit. asper* Schlotheim, pl. 1, figs. 7 a–c.
- 1820 *Terebratulites asper* Schlotheim; Schlotheim, p. 363.
- 1822 *Terebratulites asper* Schlotheim; Schlotheim, pl. 18, figs. 3 a–b.
- 1825 *Terebratula aspera* Schlotheim; Koenig, p. 3, pl. 4, fig. 44.
- 1956 *Spinatrypa aspera aspera* (Schlotheim); Struve (*partim*), p. 387, pl. 1, figs. 2 a–c.
- 1964 *Spinatrypa aspera* (Schlotheim); Biernat, pp. 309–12, pl. 4, figs. 1–5– pl. 5, figs. 1–12.
- 1964 *Spinatrypa aspera aspera* (Schlotheim); Struve (*partim*), pp. 527–9, figs. 4 a–c.

Type horizon (revised). Low Eilenberg horizon, Freilingen beds, upper Eifelian.

Range. Eilenberg through lower Nollenbach horizons.

Diagnosis. A full diagnosis of topotypic material is given in Struve (1956, p. 387).

External form. Specimens are small; maximum observed width 22 mm., maximum depth 13 mm., average width between 15 and 17 mm. (text-fig. 5). Shell valves are nearly equally convex. Anterior fold weak. The pedicle valve is slightly less convex and a bit flatter than the brachial valve. Shoulder lines straight. Lateral margins are sub-parallel,



TEXT-FIG. 5. Scatter diagrams and frequency curves of *Spinatrypa aspera aspera* (Schlotheim 1813). Scatter diagrams plotted from locality C475, MTB Mechernich r37910 : h96450. Locality C468, r38020 : h96980. Approximately Eilenberg horizon, upper Eifelian.

EXPLANATION OF PLATE 77

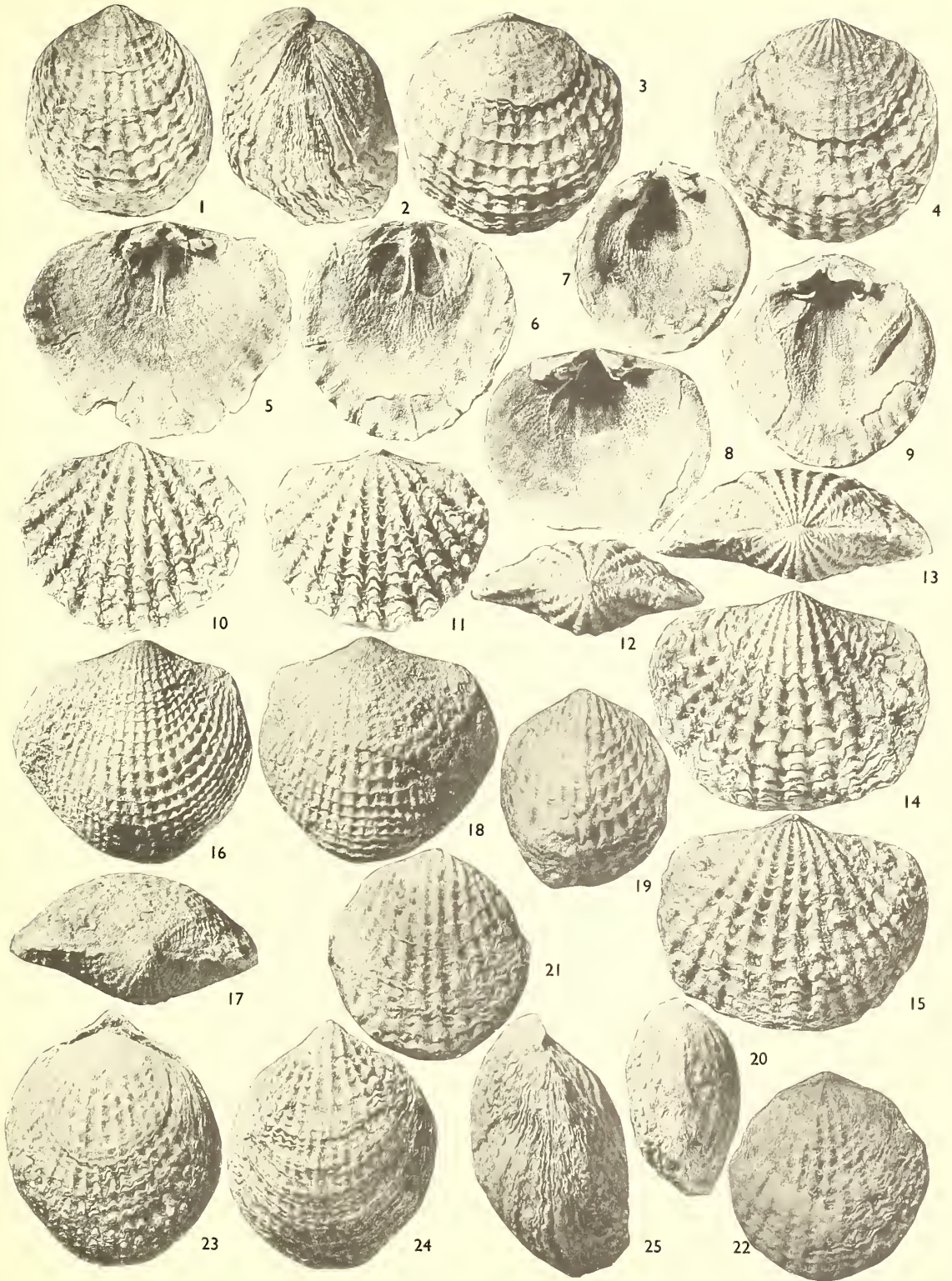
Figs. 1–9. *Spinatrypa aspera aspera* (Schlotheim 1813). Upper Eifelian, base of the Freilingen beds, MTB Mechernich r37910 : h96450 (C475). 1–2, hypotype BB55157, globose elongate variety; 3–4, hypotype BB55158, normal shell with early growth pause; 5, hypotype BB55159, brachial valve of wide variety—note elevated notothyrial pit; 6, hypotype BB55160, brachial valve of elongate variety with damaged apex; 7, hypotype BB55161, pedicle valve elongate variety—muscle scar deeply impressed; 8, hypotype BB55162, pedicle valve wide variety—small delicate tips of the crura just visible (bv); 9, hypotype BB55163, pedicle valve of elongate variety—crura visible (bv).

Figs. 10–15. *Spinatrypa aspera meridiana* n.ssp. Upper Eifelian, Nollenbach horizon. MTB Dollendorf r51000 : h75720 (C343). 10–12, paratype BB55165, small specimen; 13–15, holotype BB55166, mature form.

Figs. 16–18. *Spinatrypa cf. asperoides* Biernat 1964. Upper Eifelian, Eilenberg horizon. MTB Dollendorf r50930 : h75720 (C345). Hypotype BB55156.

Figs. 19–22. *Spinatrypa fasciplicata* (Struve 1961). Upper Eifelian, Lahr horizon. MTB Dollendorf r55530–70 : h77390 (C279f). 19–20, hypotype BB55170, small elongate, nearly biconvex form; 21–22, hypotype BB55171, somewhat flattened shell—no prominent mid-ribs; 23–25, hypotype BB55172, elongate shell with damaged umbo.

All figures $\times 2$.



COPPER, *Spinatrypa* from the German Devonian

hinge corners may be marked and angular. Hinge angles from 125 to 145 degrees. A blunt, small anacline beak normally stays free from the brachial umbo. A foramen and small delthyrium are exposed in maturity. The brachial valve is more rounded and convex but not gibbous. The dorsal apex is not exposed.

Ribs. The coarse, undulose ribs show advanced stage of disintegration and planation. Spacing of ribs at the margins is 5–6 ribs per 10 mm., favouring 5. Distally growth lamellae are thick and crowded, tending to blot out rib structure. Ribs do not show much bifurcation and intercalation and expand greatly distally.

Growth lamellae. Maximum space between lamellae in coarsely ribbed specimens is about 2 mm., but average is about 1.5 mm. Distal crowding is typical. Spines are rare, even on well-preserved material.

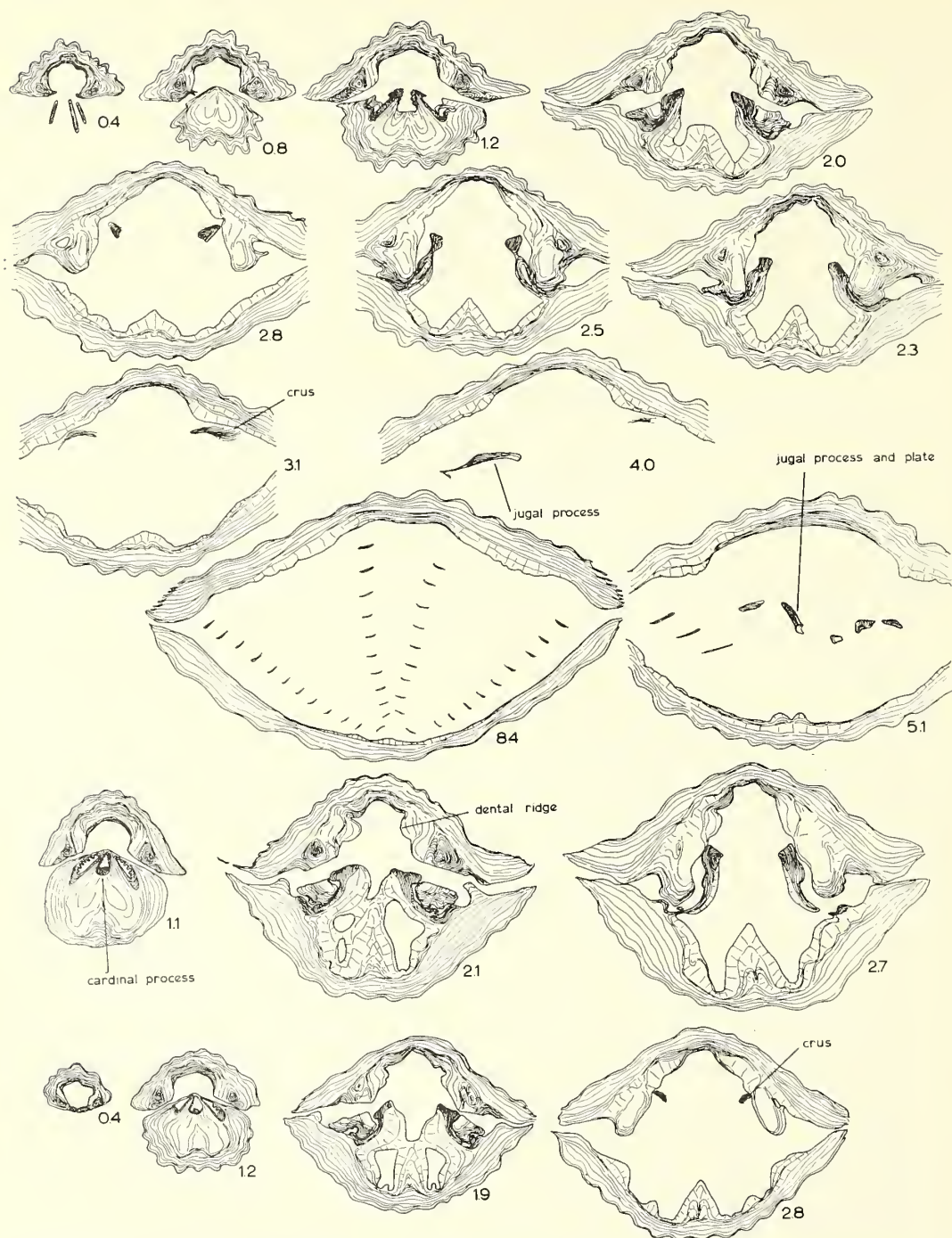
Growth and variation. Biernat (1964, p. 312) remarked that Polish specimens of this species, almost certainly conspecific, showed only limited variation. In the Eifel region, especially near the type locality, a broad dichotomy into wide, flat, and long, globose specimens seems to exist, though this did not come out in a biometrical study (text-fig. 5). Wide forms have longer and thinner areas, more orthocline than anacline beaks, a definable hinge corner, and lack globosity. Narrow forms have short areas and are gibbous in late maturity. All gradations between the two occur. However, this dichotomy is apparently absent higher in the Freilingen beds, and *Spinatrypa aspera meridiana* n.ssp., which possibly was derived from the wide variety, shows no partition of forms.

Neanic specimens are shield-shaped, with orthocline beak, a relatively much greater area, and ventribiconvexity.

Internal structure. Minute, solid deltidial plates are preserved near the borders of the delthyrial cavity. Rare distal sections of the plates show that they may be at least partially hollow. The delthyrial cavity is lined by rather thick columnar calcite. A dental nucleus broadens out into a small lateral cavity in some specimens. Teeth are short, stubby with the main lobe twisted inwardly and outer lobe strongly crenulated. A four to five stranded cardinal process caps the notothyrial pit and part of the hinge plate. Socket plates are moderately thick, outer socket ridges well marked. Thick crural bases give strong support to delicate crura which are partially feathered distally. Jugal processes are thick and distally contain nodules or small spine bases (refer to text-figs. 6–8). Jugal plates short, with small distal hooks. Spiralia with about ten whorls.

Remarks. Like *Atrypa reticularis* (Linne 1758), *Spinatrypa aspera* has gained a reputation as a catch-all species. It seems to have been found everywhere. The name *aspera* was even fixed by Koenig (1825, fig. 219) to a species of *Acanthothiris*, a spinose Jurassic rhynchonellid brachiopod. However, Koenig (1825, fig. 44) was also among the first to recognize the validity of the Schlotheim spinatrypid species.

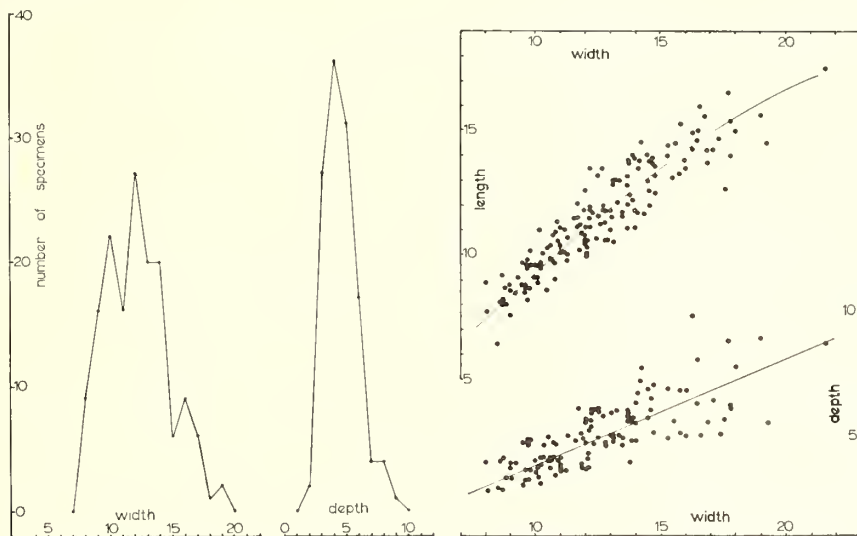
Spinatrypa aspera aspera, sensu restricto, is rare in the Hillesheim syncline but very common on the western margins of the Devonian synclines of the Eifel region. It can be distinguished from the subspecies *meridiana* in its coarser, much flatter and shallower ribs, its smaller area, greater convexity, and lack of strongly protruding orthocline beak. Struve (1964, p. 529) placed the tota species in the Rasenriff, Crinoidenwald, Knollen-blockriff milieu, but this applies only to the subspecies *meridiana*, and not to topotypical material of *aspera aspera*.



TEXT-FIGS. 6–8. Transverse serial sections of three different specimens of *Spinatrypa aspera aspera* (Schlotheim 1813). About Eilenberg horizon, upper Eifelian; MTB Mechernich r37910 : h96450. Top BB55224, middle BB55225, bottom BB55226. Note the simulated 'septalium' in the lower two globose specimens caused by angle of serial sectioning. $\times 4$.

In the Eifelian of the Prague area (Czechoslovakia), there are spinatrypids which bear a strong likeness to rare varieties of *Spinatrypa aspera aspera* from the Sötenich syncline. These Czech atrypids, *S. seniorbis* (Barrande 1847) and *S. seniorbis latecostata* (Havliček 1956) show coarse, flattened ribs and strong wide-spaced growth lamellae reminiscent of some *S. aspera* (see Pl. 76, fig. 21). In the Eifel this variety is rare.

Material. Total 3,218 specimens. The richest localities are in the Sötenich syncline and the west corner of the Blankenheim syncline and the species is virtually confined to western and northernmost parts of the Eifel sigmoid.



TEXT-FIG. 9. Scatter diagrams and frequency curves of *Spinatrypa aspera meridiana* n.ssp. Combined data from locality St621, St621a; MTB Dollendorf r52030 : h77310. Nollenbach horizon, upper Eifelian.

Spinatrypa aspera meridiana n.ssp.

Plate 77, figs. 10–15

Name. Latin, *meridianus*, southern. It is a reference to the abundance of the subspecies in the southern Eifel synclines.

Type locality. Weinberg quarry near Kerpen, Hillesheim syncline, MTB Dollendorf r53030 : h77310 (locality C343). *Type stratum.* Bohnert subhorizon (A2), Nollenbach horizon, Freilingen beds, upper Eifelian (viz. Struve 1961, p. 313).

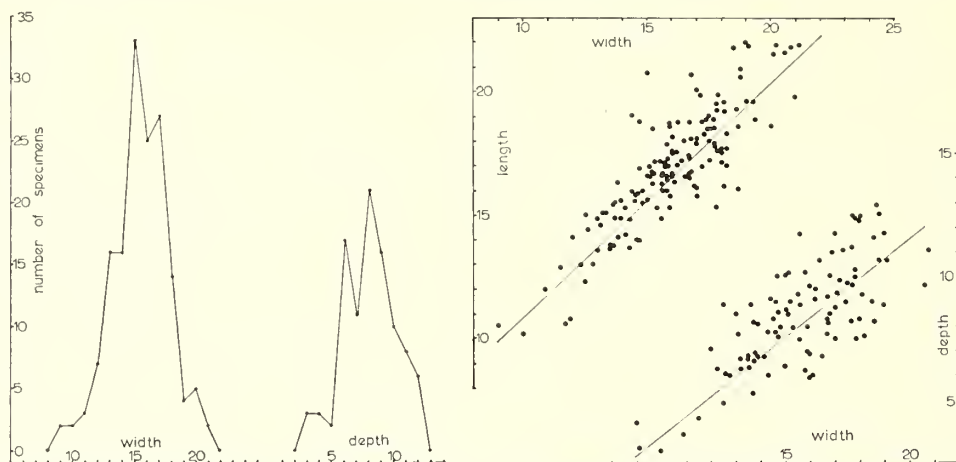
Range. Nollenbach horizon, Freilingen beds. *Source sediment.* Pale green to yellowish-brown calcareous shales and limestone interbeds. *Associated fauna.* *Atrypa* spp., *Kerpina vineta* Struve, *Carinatina plana* (Kayser), *Atryparia stabilia* Copper, *Gruenewaldtia apsaklina* Struve, *Desquamatia* sp.

Diagnosis. Small, flattish, strongly ribbed shells with well-rounded outline and wider than long. Beaks orthocline, areas small but defined, shoulder line indented. Ribs spaced at six to seven per 10 mm. marginally, imbricate (somewhat *Spinatrypina*-like), and not as interrupted as most spinatrypids. Shell somewhat flattish, with weak fold.

Remarks. There are many gradational specimens leading to an *aspera aspera* type of morphology but end members of both subspecies are distinctive (refer to Pl. 76 and Pl. 77). The new subspecies appears to be restricted to slightly younger beds. Scatter diagrams and distribution curves accentuate the differences in size and width/length/depth proportions (text-fig. 9). Compare the optimum width of 12 mm. and depth of 4 mm. with those of *S. aspera aspera*.

A striking resemblance is formed by *Spinatrypa semilukiana* (Lyashenko 1951) figured in Lyashenko (1959, pl. 51, figs. 1–2), a species of Frasnian age. The external differences between the subspecies *meridiana* and the atrypids from the Russian platform are slight.

Material. This subspecies is much scarcer in the Eifel region and only 286 specimens were examined. It is known from the Blankenheim, Dollendorf, and Hillesheim synclines.



TEXT-FIG. 10. Scatter diagrams and frequency curves of *Spinatrypa fasciplicata* (Struve 1961). Combined data from locality C279f, C279fa; MTB Dollendorf r55580 : h77390, Lahr horizon, upper Eifelian.

Spinatrypa fasciplicata (Struve 1961)

Plate 77, figs. 19–22

1961 *Invertrypa fasciplicata* Struve, pp. 334–5, pl. 2, figs. 7–8.

1964 *Spinatrypa fasciplicata* (Struve); Biernat, pp. 315–16, pl. 6, figs. 6–11.

Type locality, type stratum. In Struve 1961.

Range. Hallert and Lahr horizons (chiefly Lahr), Ahbach beds, upper Eifelian.

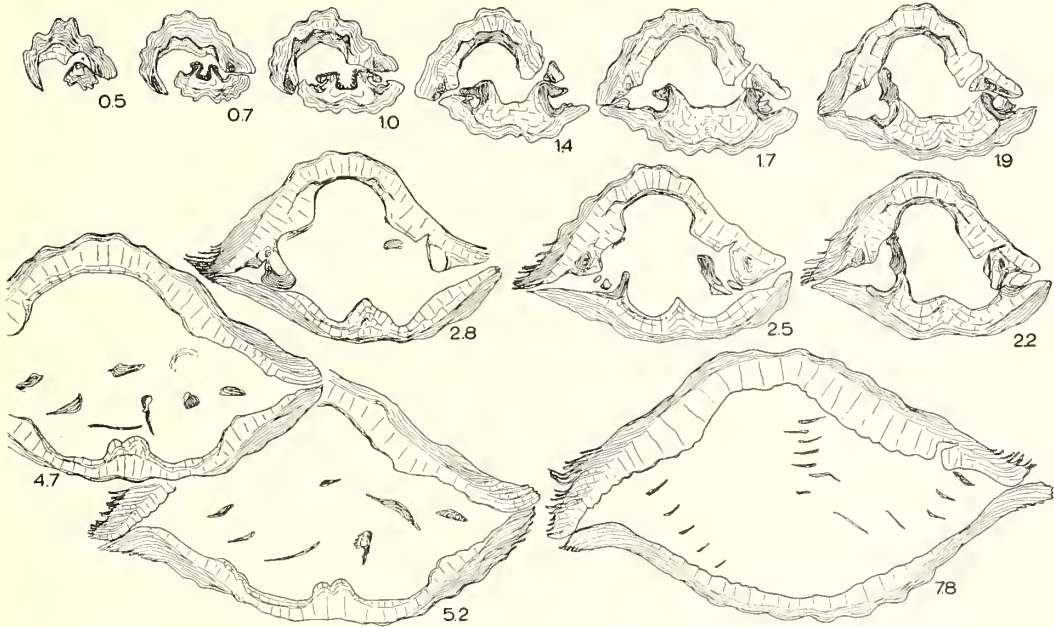
Remarks. An adequate diagnosis is cited in Struve (1961). No material has previously been sectioned. In a trench near Nohn in the Hillesheim syncline (through the type locality of the Müllert horizon), a small but decisive *fasciplicata* fauna of some 184 specimens was found (locality C279f, C279fa). Many of the specimens were crushed or deformed. Struve's original diagnosis is supplemented by statistics and serial sections.

Average width is from 15 to 17 mm. (text-fig. 10) and average depth 8 mm., thus slightly greater than for *S. kelusiana* Struve. Most specimens are longer than wide. Internal morphology compares with *S. aspera* (Schlotheim). Teeth are short, lateral

cavities absent. Crura are distal in location and supported by lengthy crural bases. Jugal processes tipped by spinose ends and thin jugal plates. About six spirallial whorls were counted.

The species on the whole is nearly equally convex, though the pedicle valve tends to be deeper. Ribs are finer, not as flattened, and interrupted by more growth lamellae than in *S. kehusiana*. Beaks are not as hypercline. Refer to text-fig. 11.

Material. Total 191 specimens. In the Eifel region, the species is virtually confined to the Hillesheim syncline, but has been reported from the Sötenich syncline (Paulus 1961) and Prüm syncline (Struve 1961).



TEXT-FIG. 11. Transverse serial sections of *Spinatrypa fasciplicata* (Struve 1961). Lahr horizon, upper Eifelian; MTB Dollendorf r55580 : h77390. Specimen slightly skew and fractured. BB55227. $\times 4$.

Spinatrypa kehusiana Struve 1956

Plate 78, figs. 1–8

1956 *Spinatrypa kehusiana* Struve, pp. 383–409, pl. 1–3, figs. 1, 3–24.

1961 *Invertrypa kehusiana* (Struve); Struve, p. 334, pl. 2, figs. 9–11.

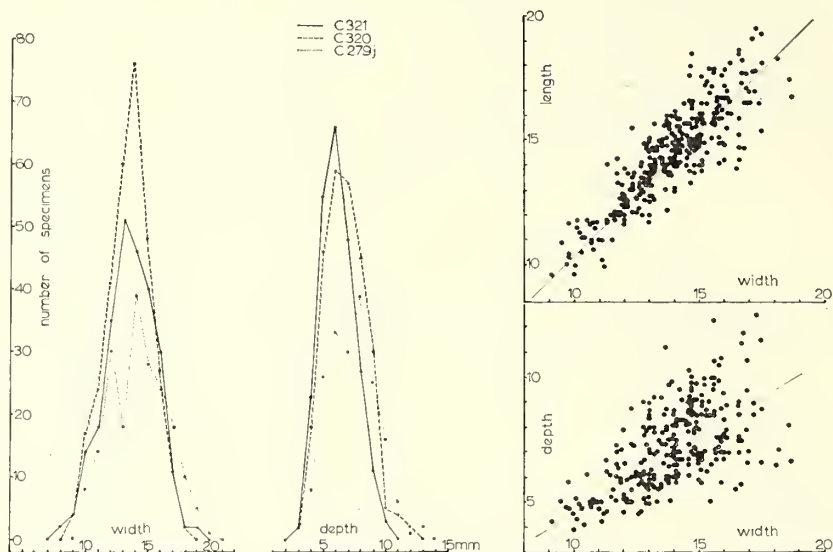
Type locality, type stratum. In Struve 1956.

Range. Müllert horizon, Ahbach beds, upper Eifelian.

Diagnosis, external form. These are given in great detail in the original description. Scatter diagrams and frequency curves confirm Struve's findings about shape variation (text-fig. 12).

Internal structure. Struve (1956) omitted details of internal shell structure except in generalized 'blackened' transverse sections. Slight deviations from the earlier descriptions are noted.

Small, minute, apparently solid deltidial plates are obscured by the ventral umbo (text-figs. 13–14). The lateral cavity is tiny and elongated parallel to the shell wall. Teeth are short, blunt, tapering and flanked by a small lateral lobe. A weak cardinal process with only two small strands were noted in the notothyrial pit. Crural bases are elongated and crura are bent laterally only very close to the ventral wall. In Struve (1956, p. 396) these extended crural bases are wrongly interpreted to be crura. Crura are long, thin and compact. Jugal plates are thin, subvertical, and rather straight. They



TEXT-FIG. 12. Scatter diagrams and frequency curves of *Spinatrypa kelusiana* Struve 1956. Scatter diagram data from locality C320, MTB Dollendorf r54620 : h75700. Frequency curves C279j, r55460 : h77380; C321 r54550 : h75730. Müllert horizon, upper Eifelian.

are not connected as claimed by Struve (1956, p. 396, pl. 2, fig. 14a). Flatly conical spires bear nearly ten whorls. No spines were noticed on the coils of the spiralia and none was seen in prepared specimens with the shell wall removed.

Remarks. The ventribiconvex shell and coarse ribs make this species easily identifiable

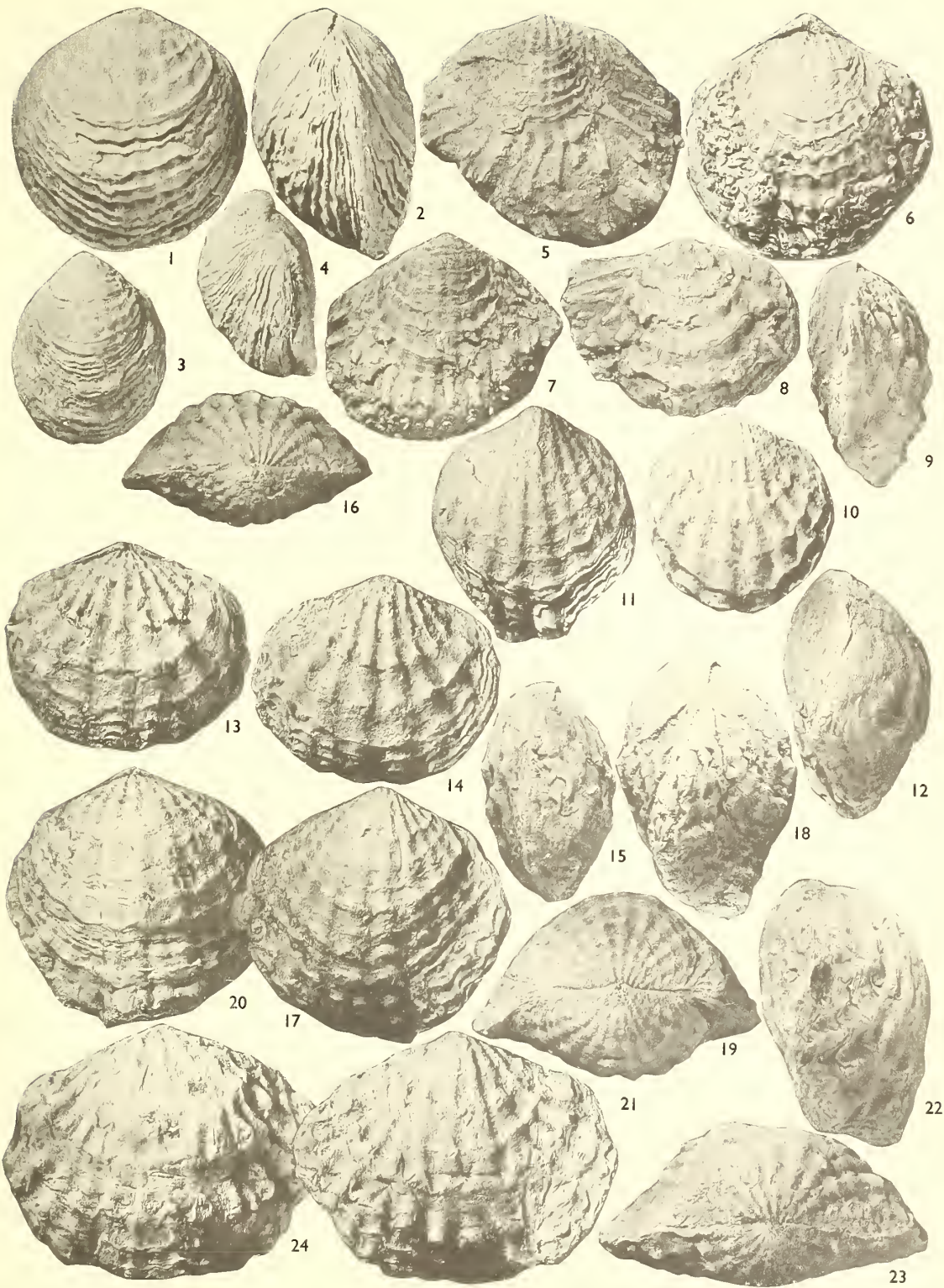
EXPLANATION OF PLATE 78

Figs. 1–8. *Spinatrypa kelusiana* Struve 1956. Upper Eifelian, Müllert horizon. 1–2, 6, MTB Dollendorf r55460 : h77380 (C279j); 3–4, r55480 : h77390 (C279i); 5, 7, 8, r54620 : h75700 (C320). 1–2, hypotype BB55183, large shell with planate ribs; 3–4, hypotype BB55177, small, elongate shell with planate ribs; 5, hypotype BB55179, ventral valve showing sturdy spines; 6, hypotype BB55182, brachial valve with attached aulopodid coral colony; 7, hypotype BB55180, ventral valve with broken distal spines; 8, hypotype BB55181, ventral valve with few preserved spines.

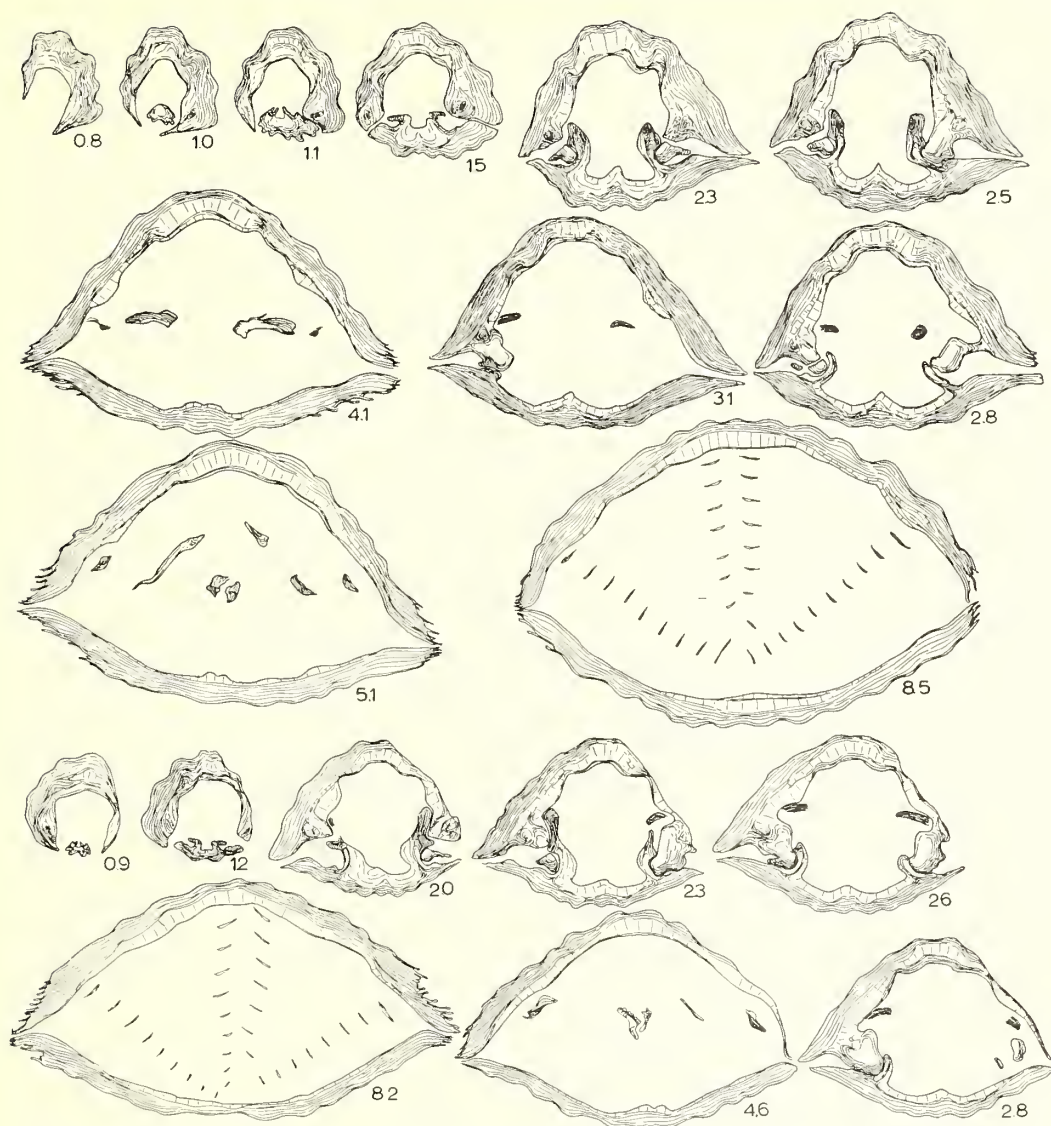
Figs. 9–10. *Spinatrypa* aff. *globulina* n.sp. Upper Eifelian, Müllert horizon. MTB Dollendorf r54550 : h75730 (C321). Hypotype BB55184, typical specimen of this rare atrypid associated with *S. kelusiana*.

Figs. 11–24. *Spinatrypa globulina* n.sp. Lower Givetian, Neuenbüsch horizon (high Wotan–low Rech). MTB Blankenheim r46410 : h90050. 11–12, paratype BB55187, elongate specimen—note mid-ribs; 13–16, paratype BB55185, small shell; 17–20, holotype BB55186, typical mature, rather globose shell; 21–24, paratype BB55188, large shell of maximum width.

All figures $\times 2$.



COPPER, *Spinatrypa* from the German Devonian



TEXT-FIGS. 13–14. Transverse serial sections of *Spinatrypa kelusiana* Struve 1956. Müllert horizon, upper Eifelian; MTB Dollendorf r54620 : h75700. Top, BB55228; bottom, BB55229. $\times 4$.

in the field. It has not been traced into the overlying, Givetian Wotan horizon but its absence there may be at least partly a feature of biotope development. The Wotan horizon contains beds rich in *Spinatrypina*, which are typical of a Rasenriff environment, and would not be expected to show a *Spinatrypa* fauna (see Copper, 1966). This biofacies change at the Eifelian–Givetian boundary detracts from the certainty that *S. kelusiana* may be confined everywhere to Eifelian rocks.

Material. Total 1,026 specimens. The species is especially abundant in the Hillesheim syncline, but rare elsewhere. Struve (1961, p. 327) has plotted its European distribution.

Spinatrypa globulina n. sp.

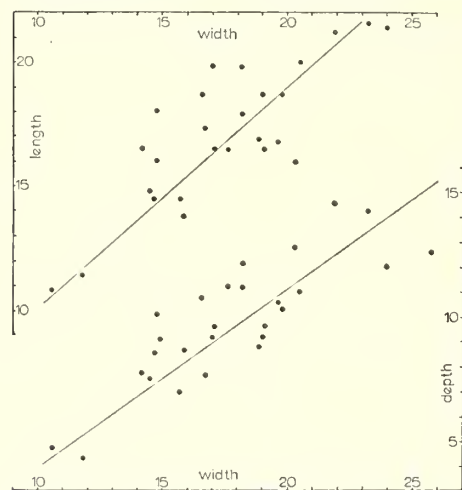
Plate 78, figs. 11–24

Name. Latin, *globus*, round ball; *ina*, diminutive, small. The shell is small and round.

Type locality. Road cut NE. Blankenheim, Blankenheim syncline, MTB Blankenheim r46410 : h90050.

Type stratum. Neuenbüsch horizon (equivalent to high Wotan–middle Rech), Loogh beds, lower Givetian.

Range. Loogh beds. Rare related specimens found in the upper Eifelian Müllert horizon (Pl. 78, figs. 9–10). *Associated fauna.* *Desquamatia ajugata* Copper, *Spinocyrtia* sp., small horn corals (*Lytho-phyllum*?), small athyrids. Fauna dominantly of *Spinatrypa* and *Desquamatia*. *Source sediment.* Greyish-green, pale brown weathering calcareous shales poor in coral fauna.



TEXT-FIG. 15. Scatter diagrams of *Spinatrypa globulina* n.sp. Loogh beds, lower Givetian; MTB Blankenheim r46410 : h90050.

Diagnosis. Small- to medium-sized, rather circular and globose shells with coarse ribs (four to five per 10 mm.) and prominent ventral mid-rib pair. Beak anacline–hypercline. Growth lamellae wide spaced. Strong anterior fold in late maturity. Internally there are distinct lateral cavities, slender teeth, and hinge plates.

External form. Mature average size falls in the 18–20 mm. range of width. Rare specimens reach 25 mm. Shells are about equally wide as long. Width/depth ratio comes to 1.9 : 1, but tapers to 1.8 : 1 in late maturity (text-fig. 15). Shell outline rounded, rarely elongate transversely or longitudinally (rare shells remind of *S. kelusiana*, e.g. Plate 78, figs. 10–11). Brachial valve slightly more convex. Beak blunt, broad, anacline to hypercline. Shoulder line weakly indented. Apical angle 125–130 degrees. Area not

well exposed except in smaller specimens, though shells from the Wachtberg horizon of the Sötenich syncline show a somewhat larger area and more anacline beak. Foramen minute, not marked. Deltidial plates usually not observed superficially. Fold narrow, incised, U-shaped. Dorsal apex covered.

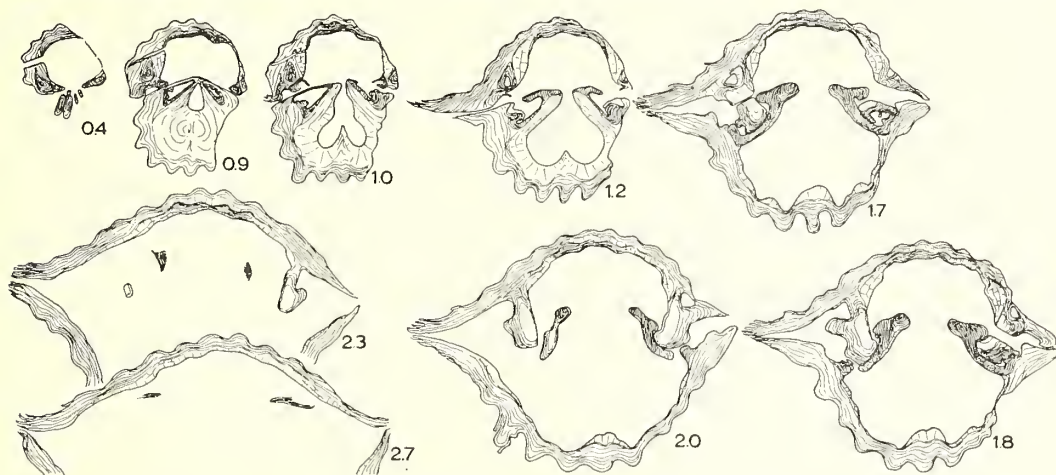
Ribs. Rounded, undulose, and broad ribs cover the shell. At the margin they have a wave length of 2.0–2.5 mm.; most are about 2.5 mm. In appearance the ribs span the variation between *S. kelusiana* (though lacking the extreme planation of some of those) and *S. curvirostra* n.sp. (but not as well defined as this form). Ribs show strong row arrangement; fragmented shells or decorticated shells give a prominent nodose appearance. Rare spines were observed: these are thick basally (1.0–1.5 mm. diameter), but their full length is not known. From the elevation of the ribs at each lamellar intersection, the spines appear to be strongly deflected, perhaps from 60 to 90 degrees on the brachial valve. Spines do not reach the abundance or prominence of *S. curvirostra* n.sp.

Growth lamellae. Growth lamellae are spaced widely at 3.5–4.5 mm. No distal crowding

was noted. Spines appear to begin at 1–2 mm. away from the shell surface. The lamellae are not extended as frilly margins like in *S. curvirostra* n.sp. and some *S. orthocline* n.sp. but tend to hug the shell surface.

Growth and variation. Smaller specimens are biconvex or ventribiconvex, with orthocline–anacline beaks. Small delthyrium and apical foramen are exposed. Incurvature to the epicline stage is common in maturity. Rare specimens retain an anacline beak.

Variation is rife. Some specimens are similar to *S. kelusiana* in their elongate shape, ventribiconvexity, and strong mid-rib pair, but already show more ‘advanced’, undulose



TEXT-FIG. 16. Transverse serial sections of *Spinatrypa globulina* n.sp. Loogh beds, lower Givetian (Neuenbüsch horizon); MTB Blankenheim r46410:h90050. Spiralia missing in this specimen. BB55230. $\times 4$.

rib-structure. Others show strong links to the younger *S. curvirostra* in beak incurvature, size, and dimensions.

Internal structure. Small deltidial plates are retracted inside the delthyrial cavity, and are hollow. Lateral cavities are clear-cut. Teeth long, flanked by small lateral lobes. A broad notothyrial pit divides thin hinge plates. Inner socket ridges thick. Crural bases and crura small, shortened. Jugal processes and spiralia not observed.

Remarks. Comparisons with *S. kelusiana* and *S. curvirostra* have been discussed. *S. globulina* is almost certainly a forerunner of *S. curvirostra*.

The species is nearly twice as coarsely ribbed and much larger and globose than *S. aspera* (Schlotheim). With its robust size and shape it is also easy to distinguish from the *S. semiorbis* (Barrande) group of Czechoslovakia, and *S. bifidaeformis* (Chernyshev).

In size, and also nearly in shape, the best comparison is with specimens illustrated by Lyashenko (1959, pl. 6, figs. 8–11) and tentatively identified by that author as *Spinatrypa* ex. gr. *bifidaeformis* (Chernyshev 1887). However, the rib structure of the Russian specimens is already advanced to a *S. curvirostra* type.

Material. The species is rather rare in the Eifel region and cannot be confirmed yet from east of the Rhine. Total 104 specimens, all from the Blankenheim and Sötenich synclines.

Spinatrypa curvirostra n.sp.

Plate 79, figs. 1–13; Plate 80, figs. 1–4

1962 *Atrypa aspera* (Schlotheim); Jux, pp. 505–13, figs. 1 a–c.

Name. Latin, *curvus*, curved, bent, arched; *rostra*, beak. The strongly incurved beak is typical.

Type locality. North slope of the Wachtberg quarry near Sötenich, Sötenich syncline, MTB Mechernich r40160 : h98850. *Type stratum.* Scheid horizon (about equivalent to Felschbach horizon), Cürten beds, lower Givetian. *Associated fauna.* *Spinatrypina soetenica* (Struve) which is rare, *Yunnanella* cf. *custos* Schmidt, *Bornhardtina* sp., *Stringocephalus* sp., rare horn corals. *Source sediment.* Dark grey to brownish-weathering shales, sometimes almost black shales, with limestone interbeds.

Range. Higher parts of the Rech horizon probably through Cürten beds, lower Givetian.

Diagnosis. Medium- to large-sized, dorsibiconvex, longer than wide shells with coarse, undulose ribs and 3–4 mm.-spaced growth lamellae. Spines are commonly preserved. Beak pointed, hypercline. Anterior fold moderate. Internally, teeth are strongly crenulated with elongate lateral cavities. Jugal plates thick; spiralia with up to fifteen whorls.

External form. Average shell width is about 25 mm., average depth 14 mm., maximum observed width 35 mm. (text-fig. 17). Shells are usually longer than wide, somewhat roundish in outline. Hinge corners not well marked. Anterior fold moderate to deep. The ventral valve, slightly less convex, flattens distally and may even be slightly concave at the margins. The shell is reasonably stable, with the brachial valve nearly twice as deep as the pedicle valve. The beak is sharp, flat, slightly angularly crested, strongly incurved, and pressed against the dorsal umbo. Areas are not visible; the foramen is minute or obscured. The dorsal apex is covered for the first 2 mm.

Ribs. Ribs are gently, evenly undulose, strongly interrupted by growth lamellae. Shallow ribs are nearly ironed out just in front of each lamella, then gradually expand in height

EXPLANATION OF PLATE 79

Figs. 1–13. *Spinatrypa curvirostra* n.sp. Lower Givetian, Scheid horizon (approx. Felschbach). MTB Mechernich r40160 : h98850 (C460b). 1–2, paratype BB55194, small shell with prominent lamellar fringes; 3–4, paratype BB55191, elongate immature shell; 5–8, holotype BB55197, mature shell with a few anterior spines partially preserved; 9–10, paratype BB55193, broad-ribbed variety; 11–13, paratype BB55195, large shell showing irregular spine growth.

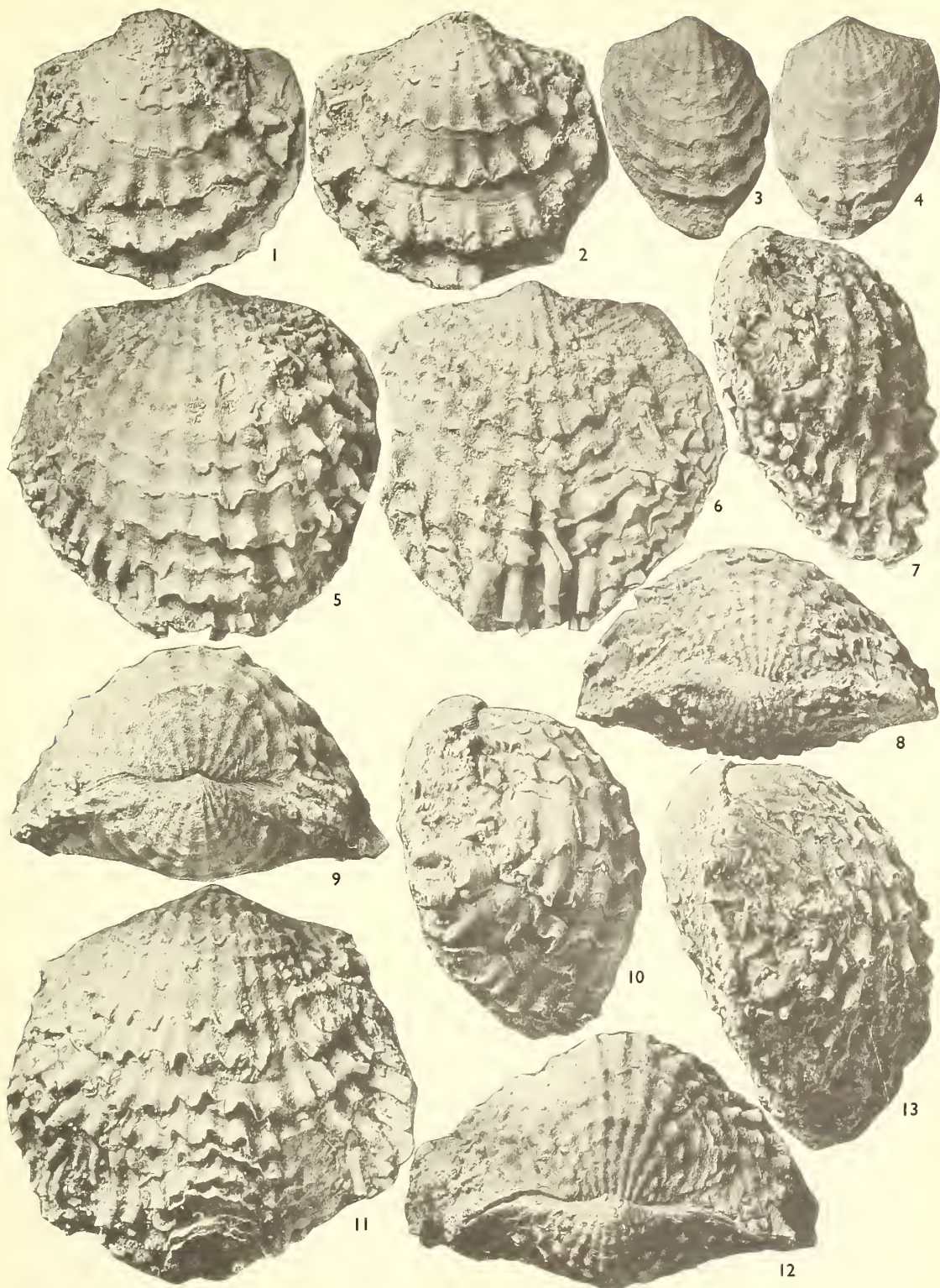
All figures $\times 2$.

EXPLANATION OF PLATE 80

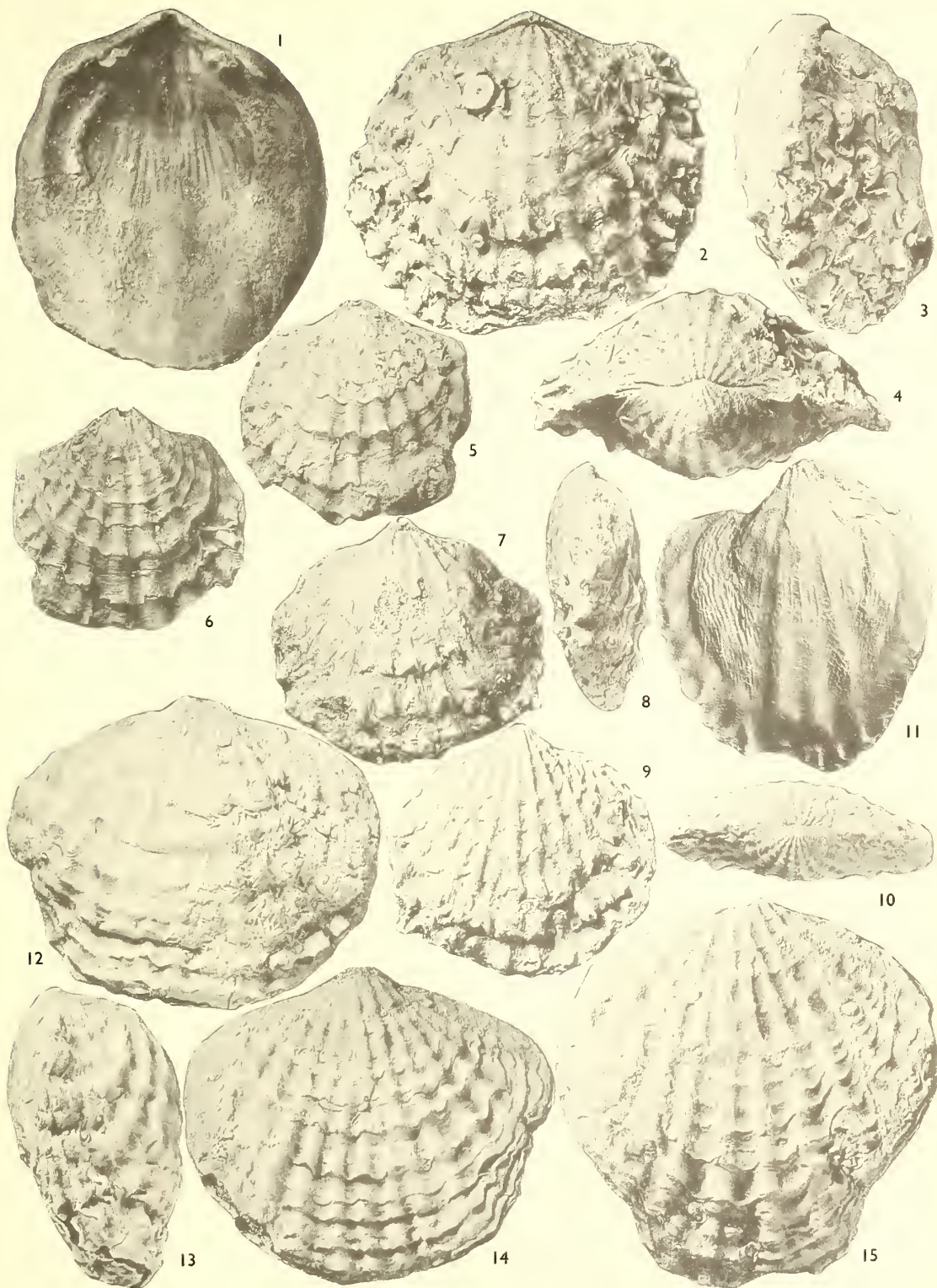
Figs. 1–4. *Spinatrypa curvirostra* n.sp. Lower Givetian, Scheid horizon (approx. Felschbach). MTB Mechernich r40160 : h98850 (C460b). 1, paratype BB55192, loose pedicle valve; 2–4, paratype BB55196, wide ribbed shell with short lamellar fringes and spines.

Figs. 5–15. *Spinatrypa orthoclinea* n.sp. Middle Givetian, Rodert beds (approx.). 5–10, 12–14, MTB Mechernich r44000 : h00370 (C454); 15, r45020 : h00840 (C453); 11, MTB Mülheim/Rhein r76800 : h51120 (C228). 5–6, paratype BB55200, immature flattish shell with broken umbo; 7–10, holotype BB55202, immature shell with typical ribs and orthocline beak; 11, paratype BB55198, decorticated pedicle valve exposing ovarian and muscle impressions; 12–14, paratype BB55203, mature broad shell with damaged umbo; 15, paratype BB55201, large shell with tongue (this variety slightly higher stratigraphically).

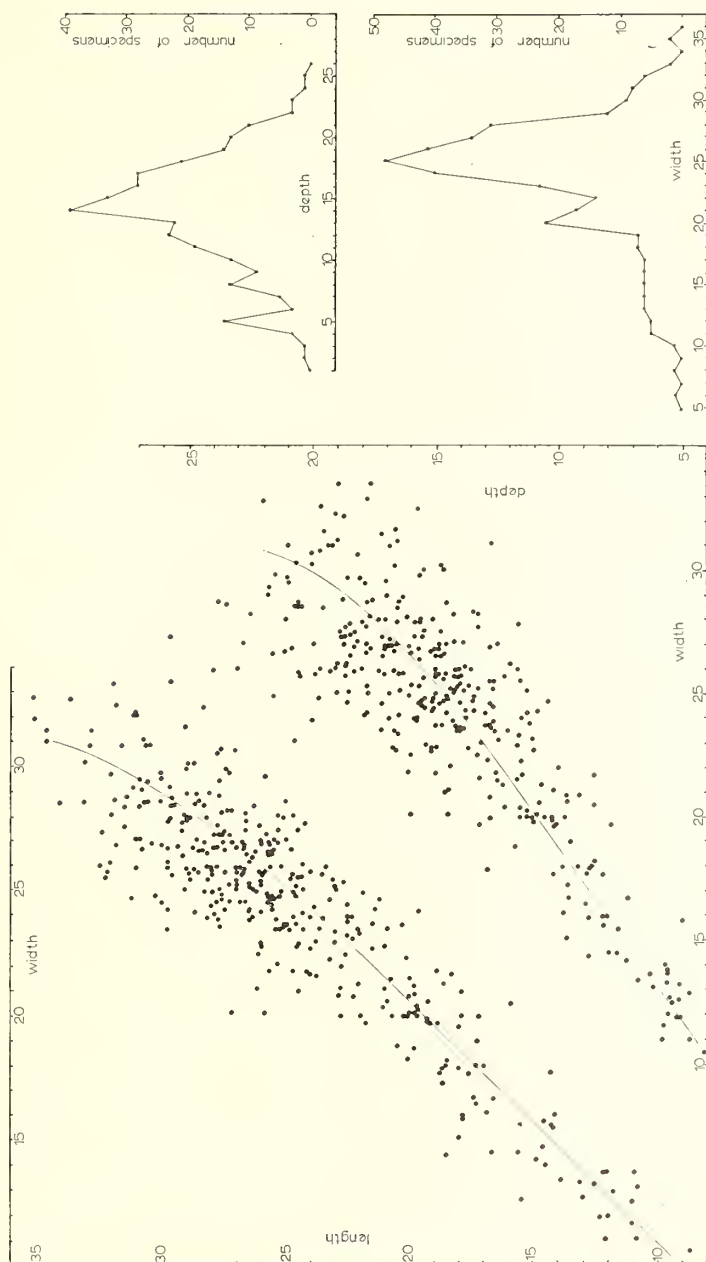
All figures $\times 2$.



COPPER, *Spinatrypa* from the German Devonian



COPPER, *Spinatrypa* from the German Devonian



TEXT-FIG. 17. Scatter diagrams and frequency curves of *Spinatrypa curvirostra* n.sp. Cürten beds, lower Givetian (Scheid horizon); Locality C460b, MTB Mechernich r40160 : h98850.

until at maximum amplitude a spine is given off. Some specimens have extremely shallow ribs (Pl. 79, figs. 1–2). Ribs are normally spaced at 4–5 per 10 mm. and do not expand much in size after 10 mm. from the apex. At 10 mm. from the apex there are 6–7 ribs per 10-mm. arc; at the margins, more than 4 ribs per 10 mm. is rare.

Growth lamellae. Growth lamellae are wide spaced at 3 mm. or more. Distal crowding is rare. Small portions of the lamellae are free and deflected at 10–20 degrees between rib crests; these give the illusion of frilly extensions. Spines are more common in the deeper troughed variety of shell. Distally there may be some disorder of spine array. On the pedicle valve, there are few spines on the apical mid-field. In the trough of the anterior fold, spines are better preserved, thicker and longer, and sub-parallel to the horizontal plane. Apically, short delicate spines about 3–5 mm. long are deflected at 40–60 degrees. The anterior side fields of the pedicle valve are more sparsely spinose with 10–30-degree deflected spines.

On the brachial valve, small areas about the hinge corners show short, laterally inclined spines deflected at 30–50 degrees. Anterior side fields contain spines at 20–40 degrees. The crest and mid-field of the brachial valve is devoid of spines.

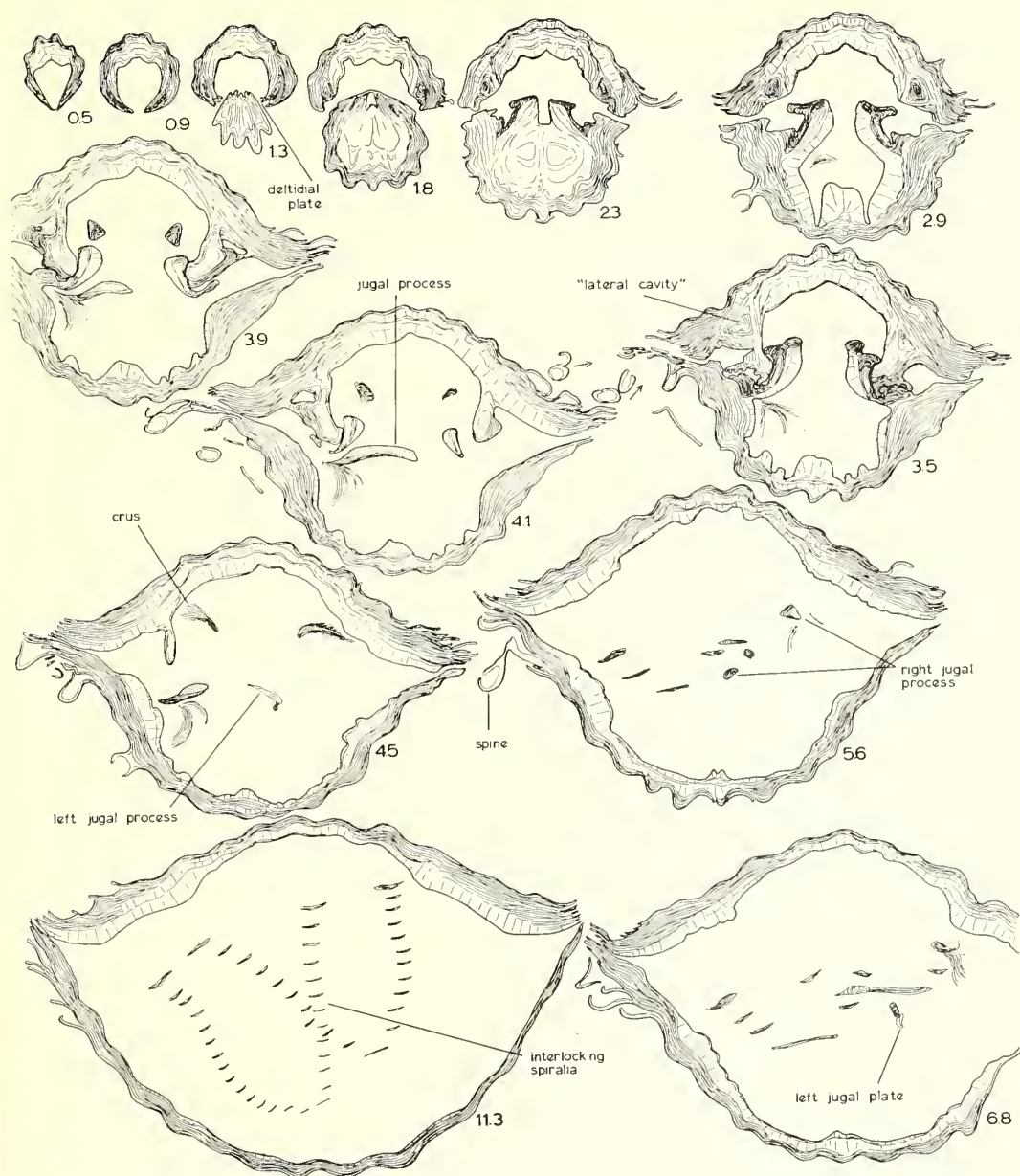
Jux (1962) dealt specifically with specimens of this species from the Sötenich syncline and reconstructed a view showing spines parallel to the commissural plane, and even some forked spines. Unfortunately, none of the nearly 800 specimens here examined, many of them well preserved, showed the spine direction portrayed by Jux (1962, fig. 1c). There is adequate evidence that the spine deflection differs sharply on the same valve and on opposing valves, and that only the spines located in the anterior trough are parallel to the commissural plane. A filter-feeding function appears unlikely.

Growth and variation. About 80 per cent. of the specimens are longer than wide and have well-defined ribs. Less common varieties include wider than long specimens (usually with flattened ribs). Some specimens show a stronger mid-rib pair than others, a feature possibly remaining from *S. kelusiana* derivatives.

Small shells (immature) are ventribiconvex, with orthocline beak, small foramen and area, and short deltidial plates. Young forms have strongly deflected spines. The foramen is obscured at an early stage.

Internal structure. Deltidial plates are small, retracted, and do not touch in maturity (text-fig. 18). Lateral cavities are rather small, elongated distally. Long teeth show centrally directed main lobes, corrugated and long lateral lobes. A small notothyrial pit contains six to eight strands of a cardinal process also overlapping the hinge plates. Crura distal, strongly feathered. Jugal processes not nodose at tips; jugal plates long and straight.

Remarks. This species has usually gone under the name *Spinatrypa longispina* (Quenstedt) in the literature of the Eifel region. As such it has been listed by Paulus (1961), Ochs and Wolfart (1961), and Hotz *et al.* (1955). From examination of topotypical material of *S. longispina*, which occurs in the Frasnian of the Boulonnais region, France, the Eifel species is seen clearly to be a distinct and separable form. This is brought out in its smaller size, finer ribs, spinose covering, and beak structure. *S. longispina* under the I.C.Z.N. should properly be referred to its Bouchard in Rigaux (1873) authorship. It was Klähn (1912, p. 31) who invalidly designated Quenstedt as the author though



TEXT-FIG. 18. Transverse serial sections of *Spinatrypa curvirostra* n.sp. Cürten beds, lower Givetian (Scheid horizon); MTB Mechernich r40160 : h98850. BB55231. Note that the spines consist of only partially closed tubes. $\times 3$.

Quenstedt (1871, p. 215, pl. 42, fig. 104) never described the species and did not even figure a complete specimen.

Spinatrypa mosolovica (Lyashenko 1952), re-illustrated in Ljashenko (1959, pl. 4, figs. 1–7), is the most similar foreign species. The Eifel form is only somewhat more

finely ribbed (with less prominent mid-ribs) and more spinose, but very likely almost coeval with the Russian species. The Eifel species may approach specimens called *S. ex. gr. bifidaeformis* (Chernyshev) by Lyashenko (1959, pl. 6, figs. 8–11) in rib structure.

Spinatrypa coriacea Crickmay (1960), from the Hume formation of north-west Canada, is larger, more flatly ribbed, and has a much more anacline beak. This Canadian species is probably of Cürten age or younger. *S. hornensis* Norris (1964) is biconvex, more deeply and less undulose ribbed, and lacks the epicline beak of Eifel forms.

Material. Total 775 specimens, mainly from the Sötenich syncline, but also from eastern parts of the Dollendorf and Hillesheim synclines. This species is also abundant east of the Rhine, near Hagen.

Spinatrypa orthoclina n.sp.

Plate 80, figs. 5–15

Name. Latin, *ortho*, straight; *clinatus*, inclined, leaning. This refers to the orthocline position of the beak in maturity.

Type locality. Road cut Urfe–Keldenich, Sötenich syncline, MTB Mechernich r44000 : h00370. *Type stratum.* Probably equivalent to the *quadrigeminum–ramosa* horizon (Hotz *et al.*, 1955) of the Rodert beds. Possibly as low as the Binz horizon, Dreimühlen beds. Middle Givetian.

Range. Tentatively assigned as Dreimühlen–Rodert, possibly more restricted or younger. *Associated fauna.* Large colonies of *Hexagonaria*, numerous *Spinocyrtia* sp., trilobites, rare thamnopods. *Source sediment.* Greenish-grey calcareous shales weathering pale brown and soft.

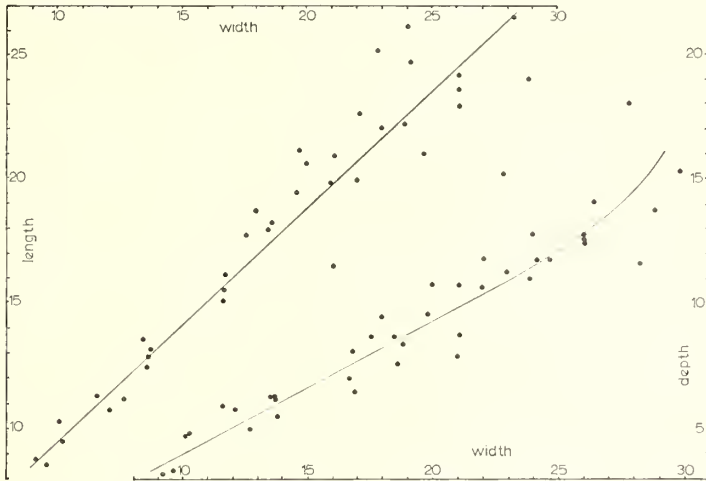
Diagnosis. Medium- to rather large-sized, coarse, and flatly ribbed shells with long projecting, orthocline beak and low anterior fold. Shell relatively flat and round-outlined, biconvex–dorsibiconvex. Internally, large lateral cavities are common, feathery crura characteristic.

External form. Average specimen width is from 23 to 25 mm., rarely up to 35 mm. (text-fig. 19). Both valves are weakly convex. Width exceeds length; width/depth ratio 2:1 : 1. On the pedicle valve, elevated mid-ribs are lacking though the mid-rib pair may be wider. Side areas are flattish and gently convex. Hinge corners poorly defined. The orthocline beak points out about 2 mm. and exposes a narrow, triangular area with deeply indented shoulder lines. Deltidial plates are small, about 1.5 mm. high and wide. The foramen very commonly expands through the apex, and is about 1 mm. in diameter. Apical angles range through 130–135 degrees. The dorsal apex is incurved and the first 1–1.5 mm. covered. The brachial valve is slightly more convex but rarely globose.

Ribs. Rib wave length is moderate: at 10 mm. from the apex, 5–6 ribs per 10 mm., at 15 mm. from the apex 4–5 ribs per 10 mm. Apical ribs are rather sharp, with steeper crests and deeper troughs. Distal ribs tend to broaden out. Large varieties may have a rib coarseness of 3 per 10 mm. Growth interruptions are marked by expansion and contraction of rib crests. At the ventral apex, a single mid-rib is flanked by 3 side ribs.

Growth lamellae. The lamellae in the apical 5–8 mm. are faint. Distal lamellae are even, spaced at 2.5 to 3.0 mm., and strongly upturned. There is little marginal crowding. Spines are rarely preserved: where present, distal spines are near-horizontal, apical spines strongly deflected. Spines are thicker and more common on the brachial valve. The longest observed spines reached 6.5 mm. They were commonly bent or twisted.

Growth and variation. Neanic specimens have a large and expansive interarea, with orthocline, weakly apsacline beak and a flat shell. They are wider than long, the brachial valve is nearly flat, and the pedicle valve slightly convex. Spines are strongly deflected. Mature specimens become more dorsibiconvex, coarse-ribbed (a lack of rib increase), and flattened. The fold is broad and may form a tongue (Pl. 80, fig. 15).



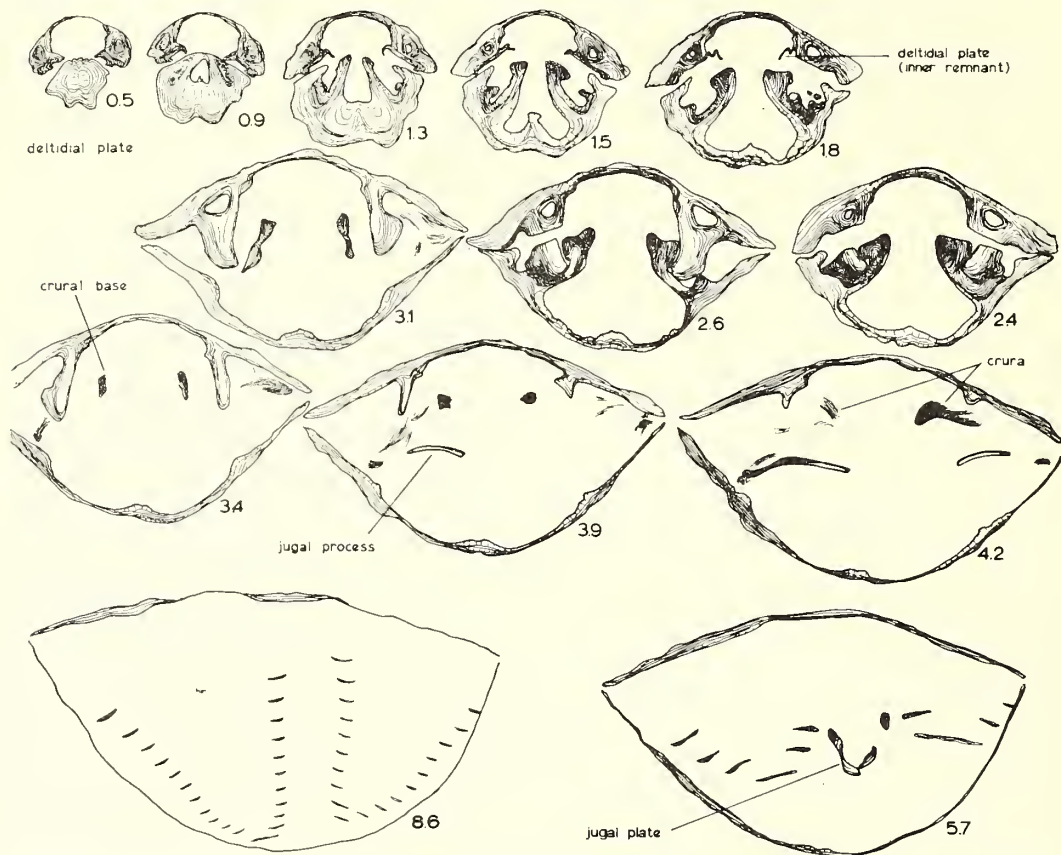
TEXT-FIG. 19. Scatter diagrams of *Spinatrypa orthochina* n.sp. Data combined from available Urfe valley localities: C454, MTB Mechernich r44000 : h00370, C453 r45020 : h00840 and BP48, BP143 (see Paulus 1961).

Internal structure. Deltidial plates hollow, with distal inner and outer portions widely apart (text-fig. 20). Inner deltidial margins are crenulated. Lateral cavities are large and oval. Teeth long, with short, thick lateral lobes. Notothyrial pit wide and broad. Cardinal process small, apparently amorphous. Hinge plates long, subvertical, evenly thickened. Socket plates bulky, crural bases elevated, crura elaborately feathered. Jugal processes are thin, weakly convex. Jugal plates long, thick, and inwardly directed. Spiralia flattened, with about ten or twelve whorls.

Remarks. There are numerous differences with *S. curvirostra* n.sp. which is an older atrypid. *S. orthochina* is planar, with more deeply incised rib and lamellar structure, a strong, pointed and orthocline beak, and lacks a marked anterior fold. Internally, *S. orthochina* is marked by large lateral cavities, long slender teeth and highly feathered crura, but particularly by its prominent hollow deltidial plates.

In 1931 Wehrli described *Atrypa aspera* var. *paffrathi* from the Paffrath syncline east of the Rhine and used material collected by a Revd. Wendland. Illustrations of this atrypid bear some resemblance to coarsely ribbed varieties of *S. orthochina* though the poor material and scant description make exact comparison unreliable. An attempt was made to collect topotypic material but this was unsuccessful. Jux (*personal communication*) also made a fruitless attempt to collect material at the site mentioned by Wehrli and concluded that an error had been made in the source locality designation, and that the atrypids probably came from Hand in the Paffrath syncline (where *S. orthochina* is

common). However, this seems unlikely for several reasons. Wehrli (1931, p. 429) mentioned that specimens were imbedded in a fine-grained dolomite, a rock type absent at Hand. Moreover, both Wehrli and Wendland later tried to find additional specimens at the locality they so precisely defined, and met with no success. It seems possible then that this atrypid was of a very local, pocket-type occurrence, a feature not uncommon for other brachiopod occurrences in the upper Givetian of this area.



TEXT-FIG. 20. Transverse serial sections of *Spinatrypa orthoclinea* n.sp. Rodert beds (approximately), middle Givetian; MTB Mechernich r44000 : h00370. BB55232. $\times 3$.

There is a likelihood that the *Spinatrypa squamosa* (Sowerby 1840) of the upper Givetian in England is conspecific with Wehrli's variety in that both are of nearly the same size and show strong rib planation. The Sowerby species is to be re-examined.

Material. Common to the middle Givetian shales east of the Rhine, but in the Eifel region can only be verified from the Sötenich syncline. Total 253 specimens.

Genus *Spinatrypina* Rzhonsnitskaya 1964

Type species. *Spinatrypina margaritoides* Rzhonsnitskaya 1964, pp. 101–3, pl. 1, figs. 1–8.

Range. Lower to Upper Devonian (Gedinnian–Frasnian).

Distribution. World-wide. *Acme.* Givetian–Frasnian.

Diagnosis. Small- to medium-sized, ventribiconvex–dorsibiconvex atrypids with ortho-cline beaks, small areas, and disjunct deltidial plates in a small delthyrium. Ribs are tubular-imbricate, deep-troughed, and embryonically spinescent. Frills lacking. Internally, pedicle layers are thin. Teeth have small to large lateral cavities. Jugal processes show short, stumpy jugal plates without spinosity or nodosity. Spiralia rarely preserved.

Remarks. The relationship of *Spinatrypina* to *Spinatrypa* is comparable to that of *Desquamatia*–*Atrypa*. *Spinatrypina* and *Desquamatia* show a parallel development of deeper, more tubular ribs and expansion of the interarea and deltidial plates, and internally an enlargement of dental nuclei into lateral cavities.

Spinatrypina, with its tubular-imbricate ribs and prominent beak and interarea, is readily separable from *Spinatrypa*. It also inhabits a different environment, being restricted to thamnoporid or disphyllid coral associates in a Rasenriff biotope. Rare occurrences of *Spinatrypa* in this environment are recorded (e.g. *S. aspera meridiana* n.ssp.), and these can result in deceptive homoemorphism. *Spinatrypina* itself does not occur outside a Rasenriff environment.

Spinatrypina demissa n.sp.

Plate 81, figs. 1–12

Name. Latin, *demissus*, low-lying, low down. This species is the oldest member of the genus in the Eifel synclines, occurring towards the base of the Eifelian sequence.

Type locality. Quarry along the east side of Urft creek, south of Nettersheim, Sötenich syncline, MTB Blankenheim r44690: h94770. See Paulus (1959, pl. 1, fig. 2) for a photograph of this locality. *Type stratum.* Upper 4 m. of the Urft horizon, approximately equivalent to the Schleit horizon, Nohn beds, lower Eifelian. *Associated fauna.* See Paulus (ibid.). The new species is probably described as *Atrypa reticularis* by Paulus. *Gruenewaldtia* sp., and thamnoporid corals are abundant. *Source sediment.* Brownish-green, chippy bioclastic calcareous shales rich in broken coral debris and some crinoidal fragments.

Diagnosis. Small, flat, biconvex shells with fine ribs (sixteen to eighteen per 10 mm.), interrupted by 2 mm. or more spaced lamellae. Margins are adpressed. A weak fold flexes the commissure. The beak is small, angular, and heads a narrow interarea. Shoulders are round-edged, shoulder lines indented. Shells are roundish, wider than long, with the pedicle valve slightly more convex. Internally (text-figs. 21–22), thin teeth are built about relatively large lateral cavities. Cardinal process thick and bushy. Columnar shell layer is thin.

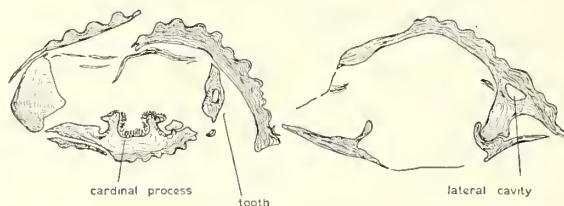
Remarks. This species is not abundant in the Eifel synclines except locally, e.g. the type locality. This is probably because of the general absence of thamnoporid thickets in lower Eifelian time in the Eifel. It can be distinguished from younger species by its fine ribs, flatness and wideness, and pointed beak. The nature of the rib-lamellae structure causes a greater affinity with some specimens of the *Atrypa* type than *Spinatrypa* type. The growth lamellae in this form are very prominent and even slightly frilly and free from the surface.

Biernat (1964, p. 317, pl. 7, figs. 1–6) described a somewhat comparable species

Desquamatia varistriata which possibly also can be referred to *Spinatrypina*, rather than *Desquamatia*. There are, in the Eifel region, older Devonian species of *Desquamatia* which do not show the trigeneric convergence (*Atrypa*, *Desquamatia*, and *Spinatrypa*) claimed by Biernat for the Polish species. A clear example is *Desquamatia ovata* Copper.

In its rib structure and general shape *Spinatrypina demissa* also is reminiscent of the genus *Kerpina* but internally shows none of the morphological peculiarities of deltidial plates, collars, and solid teeth of that later Eifelian atrypid.

Material. Total 162 specimens. The Sötenich syncline, Ahrdorf syncline, and Hillesheim syncline (central and eastern Eifel) have provided the bulk of material.



TEXT-FIGS. 21–22. Random transverse umbonal sections of two specimens of *Spinatrypina demissa* n.sp. About Schleit horizon (Urft horizon, Paulus 1959), lower Eifelian; MTB Blankenheim r44690 : h94770. Left BB55233; right, BB55234. $\times 4$.

Spinatrypina fabaca n.sp.

Plate 81, figs. 13–22

Name. Latin, *faba*, bean; *acus*, pertaining to. These small atrypids distantly resemble beans at rich localities.

Type locality. Exposure on the north flank of Leukersberg in the town of Rohr, Rohr syncline, MTB Aremberg r52360 : h91090. Locality temporarily exposed during construction work, 1963. *Type stratum.* Directly above the Rohr *Hexagonaria* horizon, even imbedded among large coral colonies (equivalent to Rechert horizon. Note that previously the Rohr horizon has been correlated with the Giesdorf horizon), Junkerberg beds, middle Eifelian.

Range. Junkerberg beds. *Associated fauna.* Colonies of *Hexagonaria*, thamnoporids, rare *Desquamatia* sp., small athyrids. *Source sediment.* Light brown or yellowish calcareous shales.

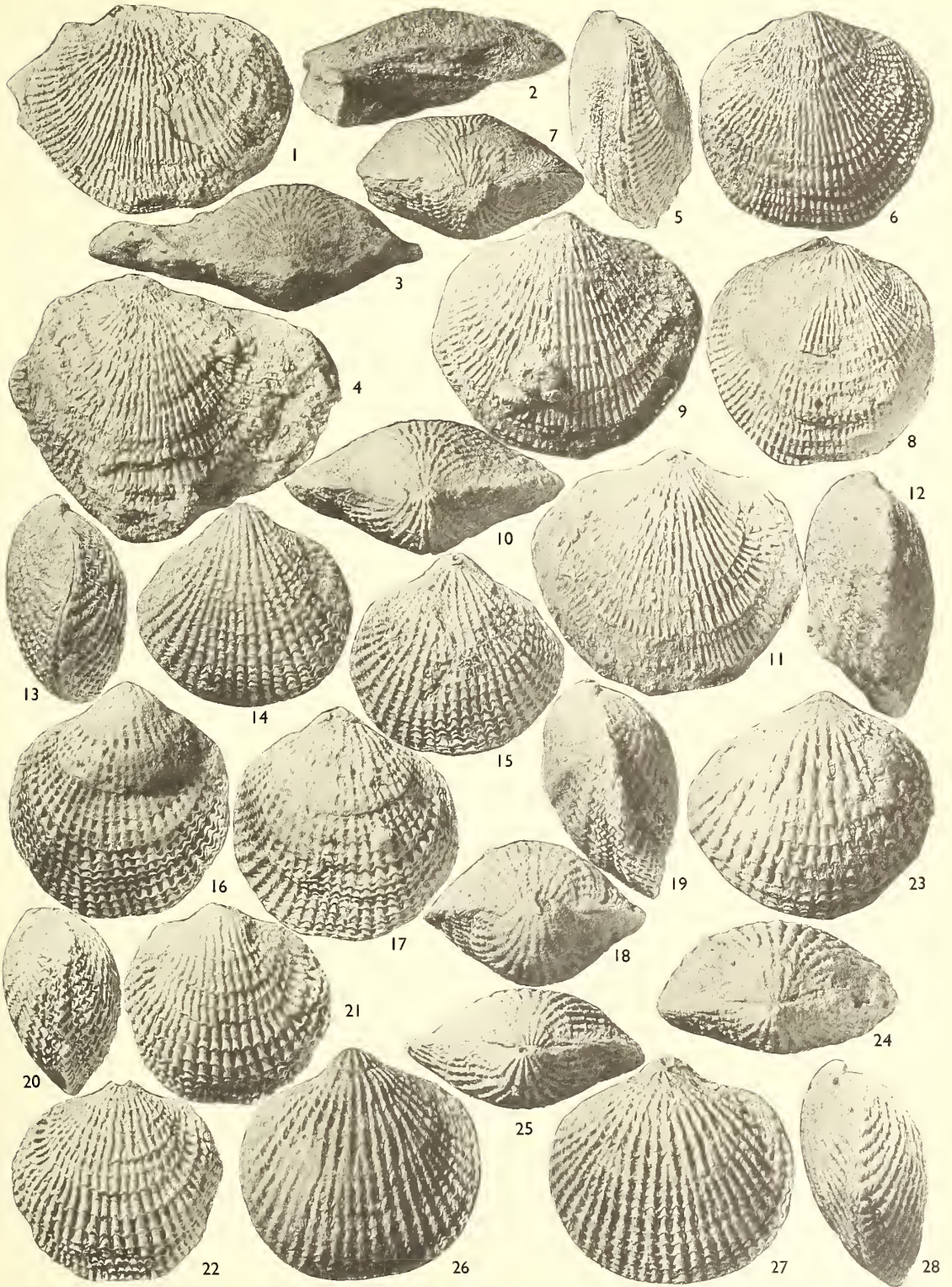
EXPLANATION OF PLATE 81

Figs. 1–12. *Spinatrypina demissa* n.sp. Lower Eifelian, Weilersbach–Schleit horizons. 1–4, MTB Blankenheim r44690 : h94770 (C451); 5–8, MTB Dollendorf r56950–7020 : h78210–50 (Fp1262); 9–12, MTB Dollendorf r56900 : h78130. 1–2, holotype BB55204, damaged specimen from type locality; 3–4, paratype BB55207, larger damaged shell; 5–8, paratype PC136, partly damaged shell, displaying tubular-imbricate ribbing; 9–12, paratype BB55206, *Spirorbis* attached to normal shell.

Figs. 13–22. *Spinatrypina fabaca* n.sp. Middle Eifelian, about Rechert horizon. MTB Aremberg r52360 : h91090 (C340). 13–15, holotype BB55208, well-preserved mature form; 16–19, paratype BB55209, long and globose shell with anacline beak; 20–22, paratype BB55210, mature shell with damaged umbo.

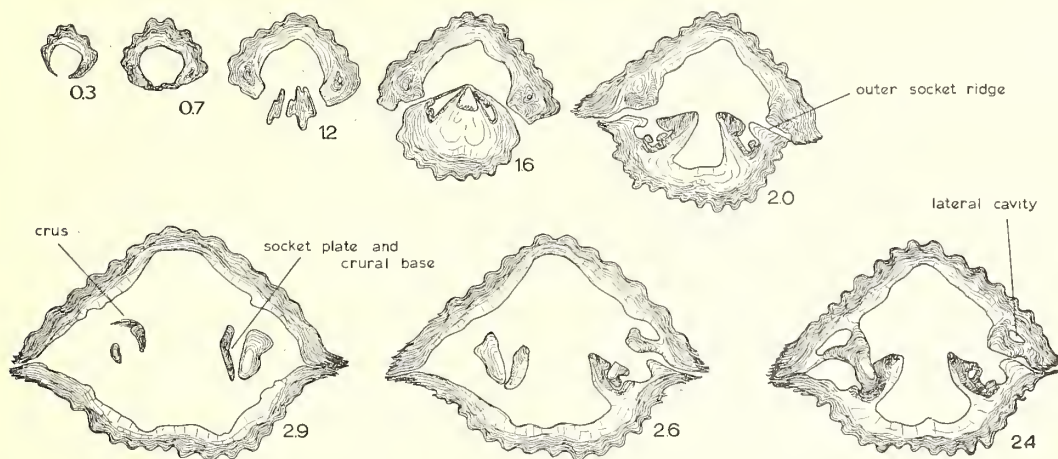
Figs. 23–28. *Spinatrypina wotanica* (Struve 1964). Lower Givetian, Wotan–Rech horizons, 23–24, MTB Dollendorf r52550–620 : h76745–800 (St739); 25–28, r54855–730 : h77060–310 (St805). 23–24, hypotype PC143, coarsely ribbed specimen of Wotan age; 25–28, hypotype PC144, finely ribbed shell of Rech age.

All figures $\times 2$.



COPPER, *Spinatrypina* from the German Devonian

Diagnosis. Small, less than 20 mm. wide, ventribiconvex–biconvex globose shells with a weak anterior fold. Beaks pointed, orthocline: foramen commonly expanded, with small anterior rim. Areal edges rounded. Shell roundish, longer than wide. Pedicle valve swollen, slightly more convex or equally convex than the opposite valve. Ribs spaced at ten per 10 mm., constant. Growth lamellae at 1–1.5 mm., crowded anteriorly. Internally (text-fig. 23) the lateral cavity is elongated, teeth long, sub-vertical with minor lateral lobe. Crura thick. Spiralia and jugal processes still unknown.



TEXT-FIG. 23. Transverse serial sections of *Spinatrypina fabaca* n.sp. About Rechart horizon, middle Eifelian; MTB Aremberg r52360 : h91090. BB55235. $\times 4$.

Remarks. The species can be distinguished by its shape, outline, and rib size from the older *Spinatrypina demissa* and the younger *S. wotanica*.

The most similar morphology belongs to *Spinatrypina sineusis* (Kayser 1883) from Ta-kwan, China. Kayser's collection of this species, which is stored in the Paläontologisches Museum der Humboldt Universität, Berlin, was examined. The Chinese atrypid is larger, more distinctly ventribiconvex, almost planoconvex, and has a smaller, less distinctive beak and area.

Spinatrypina bodini (Mansuy 1912) from North Vietnam, is larger and more coarsely ribbed than the Eifel species.

Material. Total 404 specimens. The species is common in the Rohr, Hillesheim synclines but rare elsewhere in the Eifel.

Spinatrypina wotanica (Struve 1964)

Plate 82, figs. 23–28; Plate 83, figs. 1–4

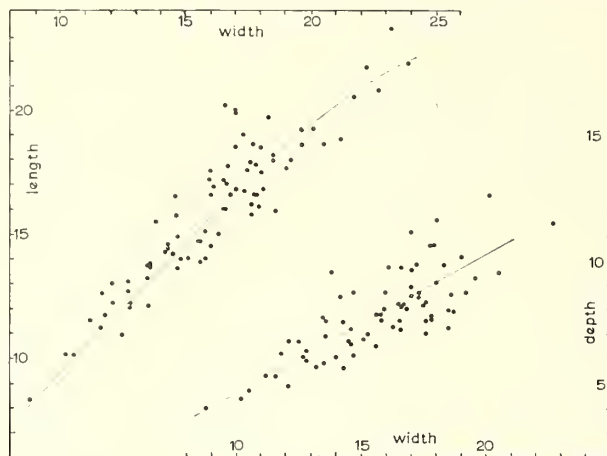
1964 *Spinatrypa aspera wotanica* Struve, pp. 529–30, figs. 2a–c.

Diagnosis. Refer to Struve 1964.

Remarks. The structure and form of the ribs and growth lamellae of this atrypid is typical of *Spinatrypina*. Ribs are imbricate-tubular and the area is well defined and sharp.

Resemblances to *Spinatrypa aspera* are apparently superficial but can give rise to confusion. Dimensions are summarized in text-fig. 24.

Material. Total 442 specimens. This species is only known abundantly from the Hillesheim syncline, where it is found in beds showing current-oriented lumachelles (see Pl. 83, figs. 9–10). Rarer occurrences are from the Blankenheim syncline.



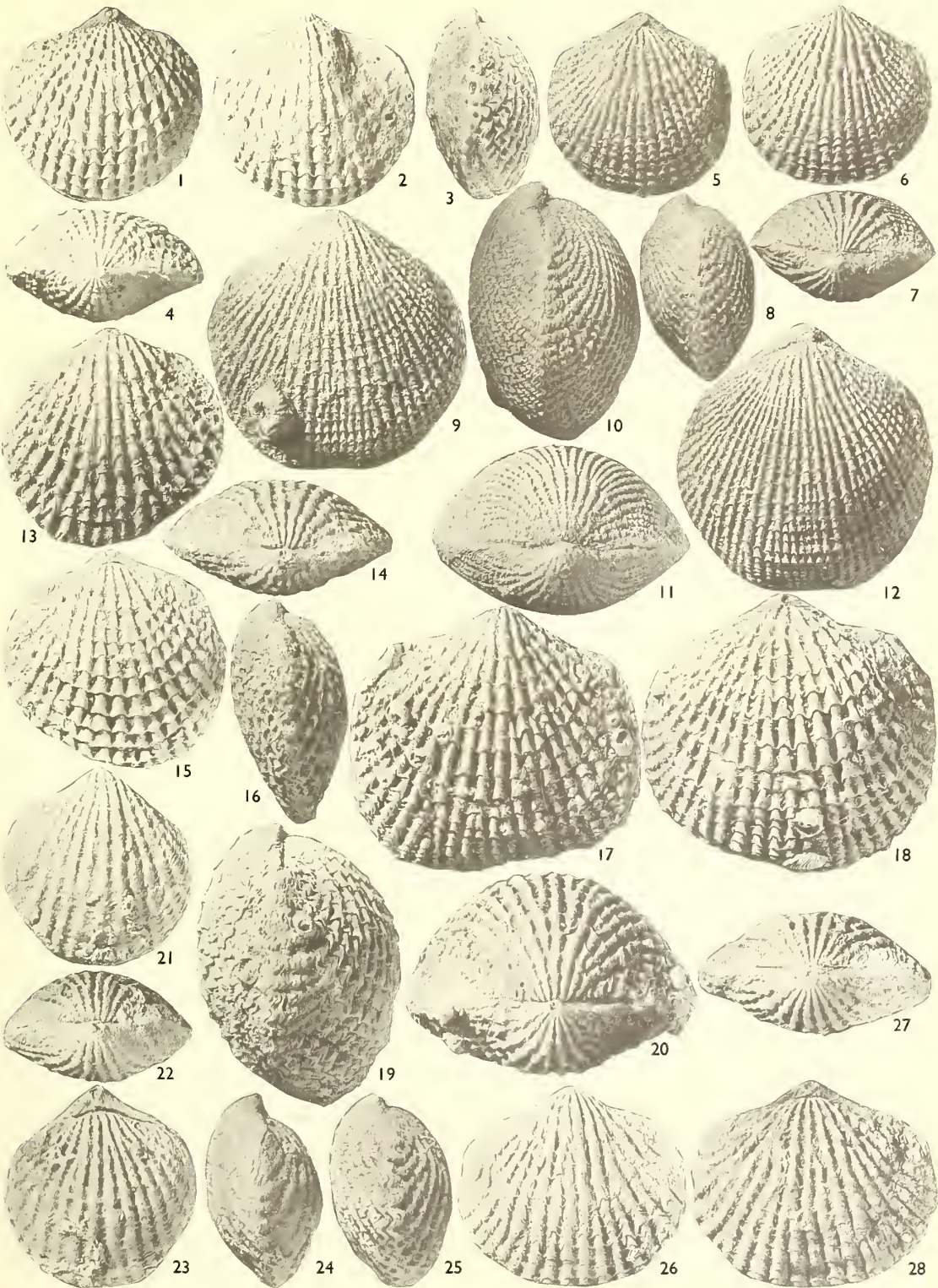
TEXT-FIG. 24. Scatter diagrams of *Spinatrypa wotanica* (Struve 1964). Locality St739, Rech horizon, lower Givetian; MTB Dollendorf r52550 : h76745, r52620 : h76800.

EXPLANATION OF PLATE 82

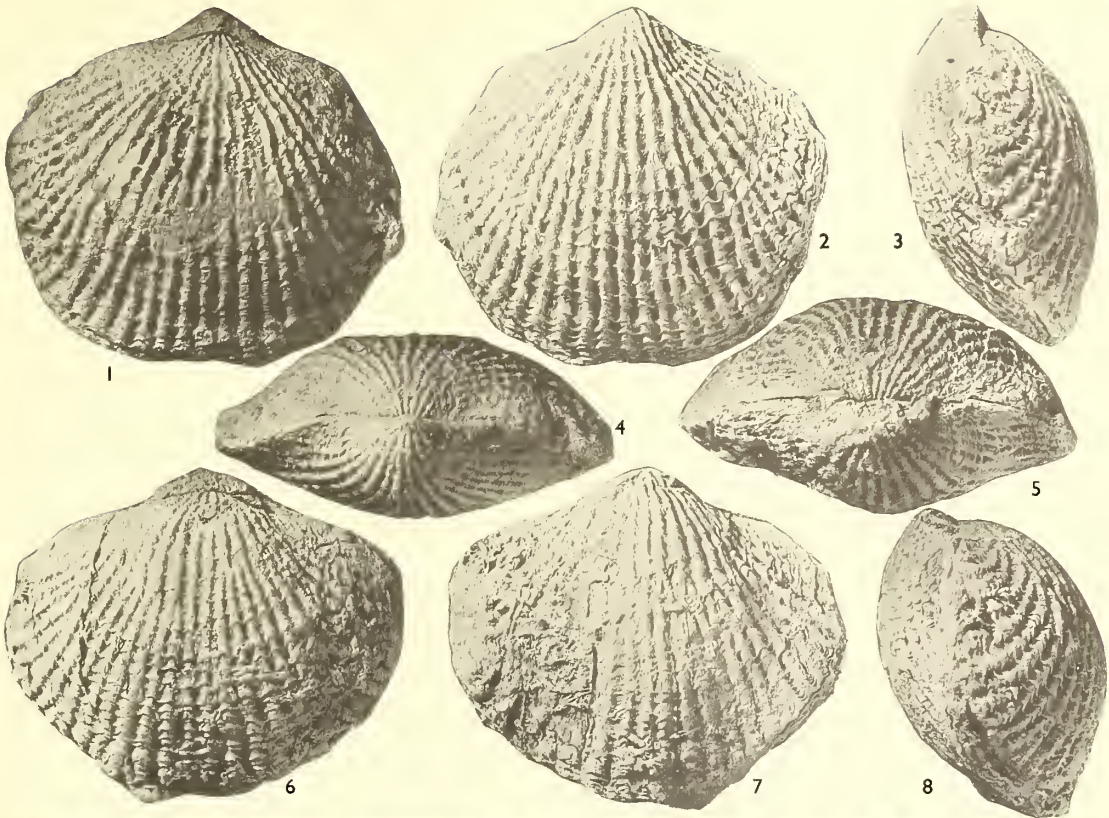
- Figs. 1–4. *Spinatrypa wotanica* (Struve 1964). Lower Givetian, Rech horizon. MTB Dollendorf r54815 : h77240 (St804). Hypotype PC142, smaller immature shell (compare figs. 13–20).
 Figs. 5–12. *Spinatrypa soetenica* (Struve 1964). Lower Givetian, Felschbach horizon. MTB Mechernich r40160 : h98860 (C460a). 5–8, hypotype BB55217, typical immature form; 9–12, hypotype BB55218, adult shell.
 Figs. 13–20. *Spinatrypa* cf. *soetenica* (Struve 1964). Lower Givetian, Felschbach horizon. MTB Mechernich r40160 : h98860 (C460a—accompanying typical *S. soetenica*). 13–16, hypotype BB55215, flattish immature shell; 17–20, hypotype BB55216, mature shell of ribbing intermediate to *Spinatrypa*.
 Figs. 21–28. *Spinatrypa girzenensis* n.sp. Middle Givetian, about Dreimühlen beds. MTB Mechernich r41650 : h99220 (C459b). 21–24, paratype BB55220, small specimen with deformed beak; 25–28, holotype BB55219, specimen slightly smaller than average mature size.
 All figures $\times 2$ unless otherwise stated.

EXPLANATION OF PLATE 83

- Figs. 1–8. *Spinatrypa girzenensis* n.sp. Middle Givetian, about Dreimühlen beds. MTB Mechernich r41650 : h99220 (C459b). 1–4, paratype BB55221, rare large variety showing trend towards *S. tubacostata* (Paeckelmann 1913); 5–8, paratype BB55222, globose and wide variety.
 Figs. 9–10. *Spinatrypa wotanica* (Struve 1964). Lower Givetian, Rech horizon, Loogh beds, MTB Dollendorf r54550 : h77780. BB55287. 9, upper side of a 3.5 cm.-thick limestone slab with a coquina of loose pedicle and brachial valves, washed into a convex-side up stable position. Note a few small athyrid brachiopods, crinoid ossicles, and fenestellate bryozoans; 10, underside of the same slab with concave side of the shells oriented upwards. $\times 1$.
 All figures $\times 2$ unless otherwise stated.



COPPER, *Spinatrypina* from the German Devonian



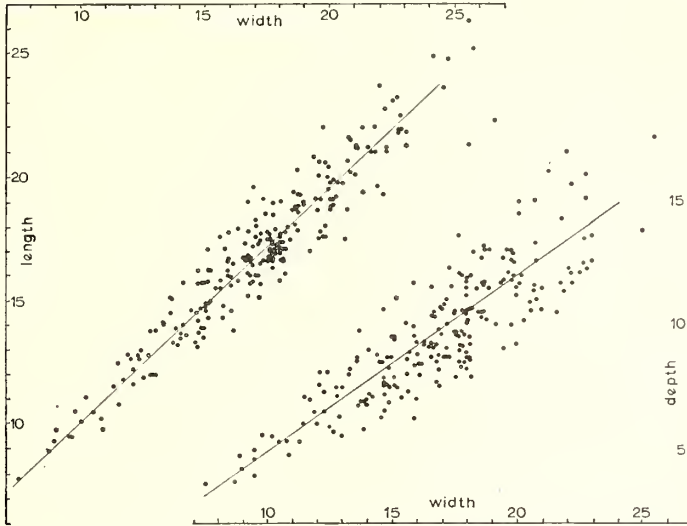
COPPER, *Spinatrypina* from the German Devonian

Spinatrypina soetenica (Struve 1964)

Plate 82, figs. 5–12

1964 *Spinatrypa aspera soetenica* Struve, pp. 530–1, fig. 3.

Remarks. As for the older species *wotanica*, this atrypid has only a distant superficial resemblance to the *Spinatrypa aspera* (Schlothheim) group. At the Wachtberg quarry



TEXT-FIG. 25. Scatter diagrams of *Spinatrypina soetenica* (Struve 1964). Locality C460a, lower Scheid horizon, Cürten beds, lower Givetian; MTB Mechernich r40160 : h98860.

where it was found in great numbers a crude separation into a larger, coarsely ribbed type and a smaller, finely ribbed type is possible. But the two varieties are presently still classed under the same name. The more coarsely ribbed form is possibly a remnant of the older *S. wotanica* (Struve). Statistically, the two types do not appear separable (text-fig. 25).

Internally (text-fig. 26: a finely ribbed, holotypic specimen), deltidial plates are small, hollow. Teeth long, lateral cavities elongated. Jugal processes not observed. Spiralia extremely scarce, and often dwarfed (e.g. text-fig. 26, section 6.2 mm.). Another specimen showed two interlocking, upside-down spiralia (text-fig. 27).

Material. Total 1,059 specimens. This species is common in the northern Eifel and east of the Rhine, but very rare in the south Eifel.

Spinatrypina girzenensis n.sp.

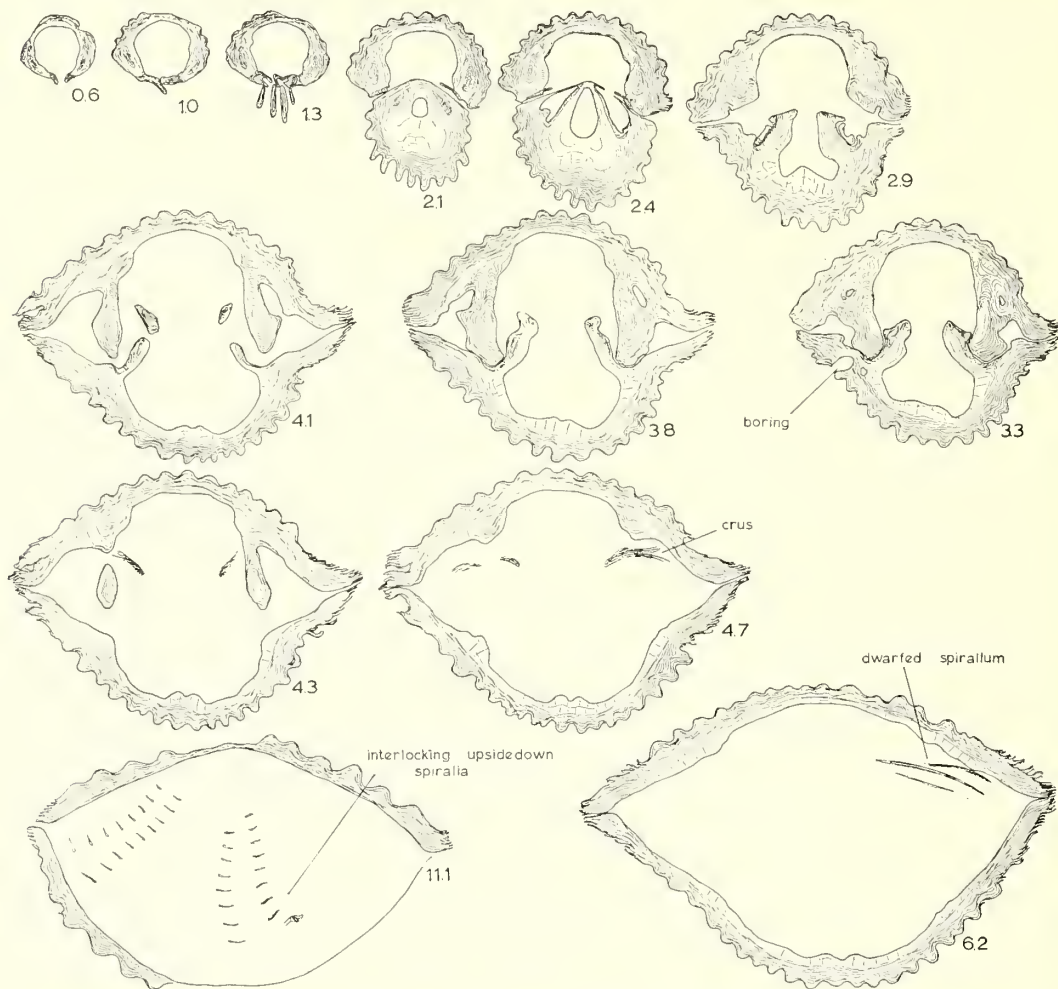
Plate 82, figs. 21–28; Plate 83, figs. 1–8

Name. After Girzenberg, a small hill about 100 m. south-west of the type locality in the Sötenich syncline.

Type locality. Road cut 1 km. south of Keldenich, Sötenich syncline, MTB Mechernich r41660; h99230.

Type stratum. Shaly interbeds between *Hexagonaria*-rich horizons, directly overlain by coarse-grained

dolomites, probably Dreimühlen beds, middle Givetian (Binz horizon?). *Associated fauna*. Small athyrids, spiriferids, numerous *Thamnopora*, *Aulocystis*, and *Roemeria* tabulate corals. Also *Hexagonaria*. *Source sediment*. Yellowish-brown calcareous shales with lumachelle heaps of brachiopods and corals (no horn corals).



TEXT-FIGS. 26-27. Transverse serial sections of *Spinatrypina soetenica* (Struve 1964). Scheid horizon, Cürten beds, lower Givetian; MTB Mechernich r40160 : h98860. One completely sectioned specimen (0.6-6.2 mm.) with a dwarfed, three-whorl spirallium, BB55236. Single section (11.1 mm.) of specimen with upside-down interlocked spiralia, BB55237. $\times 3$.

Diagnosis. Small- to medium-sized atrypids with rather coarse ribs spaced at seven to nine per 10 mm., round-outlined, frequently globose. Interareas relatively large, round-edged; beaks blunt, orthocline, strongly jutting. Growth lamellae hug the shell and are barely deflected; imbrication not noticeable. Anterior folds weak. Shells wider than long, equally convex.

Remarks. A few specimens show affinities with the *Spinatrypina tubaecostata* (Paeckelmann)—*S. explanata* (Schlotheim) group in being much wider than long, rather flat, and in having larger areas (e.g. Pl. 83, figs. 1–4).

This species is distinct from *S. soetenica* in its much coarser ribbing, its convexity, and shell-hugging growth lamellae with lack of imbrication.

Material. The species is confined to the northern Eifel and east of the Rhine in its presently known distribution. Total 1,047 specimens.

CONCLUSION

A great deal of systematic work remains to be done to refine the present species for the purpose of more detailed biostratigraphy. Internal structures need to be more thoroughly examined and interrelationships of *Spinatrypa* and *Spinatrypina* clarified. It is questionable if *Spinatrypina* represents an off-shoot from a *Spinatrypa* stock. It may well have been an independent lineage showing convergence towards characteristics of spinose atrypids. The earliest *Spinatrypina* may well have been derived from a form like *Atrypa reticularis* var. *lonsdalei* Alexander (1949, pl. 9, figs. 3a–d). *Spinatrypa*, on the other hand, was already well established in the Silurian as the illustrations of Poulsen (1943, pl. 2, fig. 14), Chapman (1913, pl. 11, fig. 15), and Davidson (1882, p. 112) show. Alexander's *Atrypa reticularis* var. *davidsoni* (1949, pl. 10, figs. 1a–d) probably also can be referred to *Spinatrypa*.

A number of Devonian European *nomina dubia* remain to be investigated. Among these are *Atrypa squamosa* Sowerby 1840, *Terebratula insperata* Phillips 1841, *Atrypa trigonella* Davidson 1884, *Atrypa reticularis* var. *sagittata* Maurer 1885, and *Atrypa aspera* var. *paffratli* Wehrli 1931, all of which may probably be grouped under *Spinatrypa*.

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PALAEONTOLOGY

VOLUME 10 • PART 3

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NEW ORDOVICIAN BOTHRIOCIDARIDAE FROM GIRVAN AND A REINTERPRETATION OF *BOTHRIOCIDARIS* EICHWALD

by C. R. C. PAUL

ABSTRACT. Five specimens of bothriocidarid sea urchins are described; one is the seventh known example of *B. globulus* Eichwald. The other four represent *Neobothriocidaris* gen. nov. characterized by having perforate plates arranged in rows and one pore of each pore-pair shared by two plates. *N. peculiaris* and *N. minor* spp. nov. are separated on the number and arrangement of spine mamela.

The holotype of *N. peculiaris* has parts of two radial water vessels preserved within the single columns of imperforate plates which have been regarded as inter-radial in *Bothriocidaris*. On the assumption that *Neobothriocidaris* and *Bothriocidaris* are closely related genetically, the single columns of imperforate plates in the latter are reinterpreted as being radial. The five apical plates become genitals with one modified as a madreporite. Growth of the corona is more readily explained and the entire columns of imperforate plates may represent oculars. Details of the peristome and jaw apparatus do not however fit the new interpretation very well.

A SINGLE specimen of a sea urchin related to but distinct from the earliest known genus, *Bothriocidaris*, was located in the Gray collection of echinoderms from Girvan now in the British Museum (Natural History). Subsequently, additional specimens were located among material collected by Mr. R. P. Tripp and sent to Professor G. Regnéll of Lund; among the Hunterian Museum collections and, after the manuscript was completed, among material loaned by Dr. A. Lamont to the late W. K. Spencer. These are referred to as the BMNH, the Lund, the Hunterian, and the Lamont specimens for convenience.

Quite independently of this Professor Regnéll had recognized and prepared a manuscript on a single example of *Bothriocidaris* ss. among the Tripp collection. With characteristic generosity he made the specimen and photographs available to the present author so that a complete record might be made. The author is also indebted to Dr. R. P. S. Jefferies and Mr. H. G. Owen, British Museum (Natural History) (BMNH), Dr. W. D. I. Rolfe, Hunterian Museum (HM), and Mr. R. P. Tripp for the loan of material. Dr. V. Jaanusson kindly loaned specimens of *Bothriocidaris pahleni*. Special thanks are due to Dr. Jefferies for a translation of Männil's paper on *Bothriocidaris*. Useful discussion and criticism have been received from Professor J. W. Durham, Dr. G. M. Philip, Dr. P. M. Kier, Dr. R. P. S. Jefferies, and Mr. A. G. Brighton. This work was completed during the tenure of a Science Research Council Research Scholarship which is gratefully acknowledged. Finally thanks are due to Professor O. M. B. Bulman for research facilities in the Sedgwick Museum, Cambridge.

DESCRIPTION OF SPECIMENS

A. The Tripp Specimen

Bothriocidaris globulus Eichwald

Plate 85, figs. 1-4

[Palaeontology, Vol. 10, Part 4, 1967, pp. 525-41, pls. 84-85.]

This specimen (Tripp Coll. 2464 a-b) consists of internal and external counterparts showing fifteen plates in three columns—two of perforate plates and a central column of imperforate plates.

External counterpart. The external counterpart (2464 a. Pl. 85, figs. 1-3) shows moulds of five imperforate plates in the central column and four and six perforate plates in the adjacent columns. The perforate plates are in definite columns and each pore-pair is entirely within a single plate. Part of the adoral half of the corona is preserved and the lowest imperforate plate is terminal in the column, the two adjacent perforate plates meeting below it. Unfortunately the 'primordial ambulacral' plates of these columns are missing.

The lowest imperforate plate is irregularly hexagonal, angular below, and 1.75 mm. wide by 2.0 mm. high. The second plate is irregularly heptagonal. Both bear a single subcentral, perforate spine mamelon about 0.3 mm. in diameter. The third plate is 2.75 × 2.05 mm., regularly hexagonal, and angular above. There are two small plates side by side above it (Pl. 85, fig. 1), and the column reaches a width of 3.65 mm. at this point. There are three perforate mamela 0.3 mm. in diameter on the third plate and one on the right-hand plate above. The left is obscured by some remaining coronal calcite.

The surface of the plates was strongly convex (concave in mould) and covered with fine asperities. The matrix has penetrated the original organic spaces in the test. The stereom network was of the usual three-dimensional arrangement of calcite rods approximately perpendicular and parallel to the plate surfaces.

In the right column there are six perforate plates all much broader than tall. The lowest is 2.0 × 0.85 mm. and the largest measurable (the fourth) 3.15 × 1.6 mm. Each has a pore-pair and peripodium medially near the lower margin of the plate. The peripodia are circular, 0.8 mm. in diameter internally and with a conspicuous rim, weaker below. The peripodium floor is weakly convex (concave in mould) with a peripheral channel connecting the two pores. A line joining the two pores of a pair meets the vertical at 28°. There are two pairs of mamela on the peripodium of each plate. Numbering the mamela clockwise from the lower left, one and two form one pair. A pair of mamela are 0.5 mm. apart, two and three are 0.6 mm., and one and four 1.0 mm., all measured centre to centre. In no plate are all four mamela perforate. When perforate they are 0.3 mm. in diameter but when imperforate only about 0.2 mm. Two plates (4th and 5th) have both perforate and imperforate mamela on their surfaces. The perforate plates are strongly convex and covered with asperities. The left column shows four plates of

EXPLANATION OF PLATE 84

Stereo-photos of *Neobothriocidaris peculiaris* gen. et sp. nov. 1, BMNH E 42523 c. 2, BMNH E 42523 b internal counterpart of E 42523 c. 3, E 42523 a. 4, E 42523 b internal counterpart of E 42523 a. 5, Detail of several loose plates in E 42523 b showing entire casts of the central pores of the perforate plates and in one plate (top centre) the cast of the terminal portion of a lateral vessel connected to the cast of a sutural pore. 6, Detail of several articulated plates of E 42523 b and three inverted plates. The lower pair of inverted plates show casts of the terminal portions of the lateral vessels connected to the casts of the sutural pores and the lower left shows part of the cast of another lateral vessel. The upper plate shows casts of three lateral vessels (to the lower right) passing into the plate beside the cast of the sutural pore.

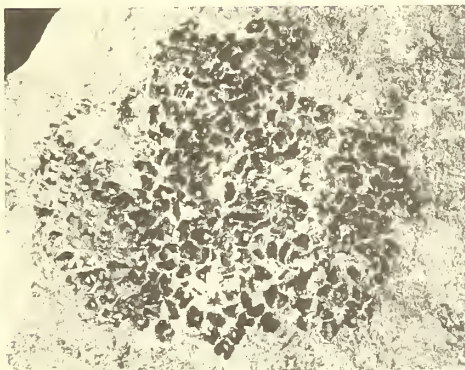
Figs. 1-4 × 2, figs. 5-6 × 5 and whitened with ammonium chloride sublimate.



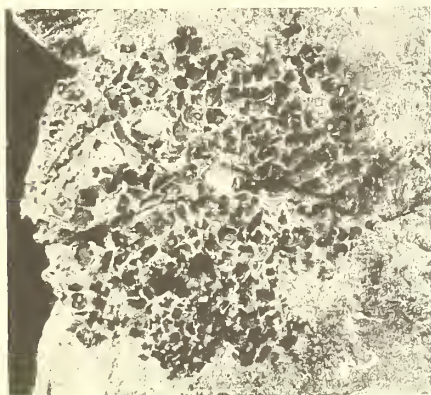
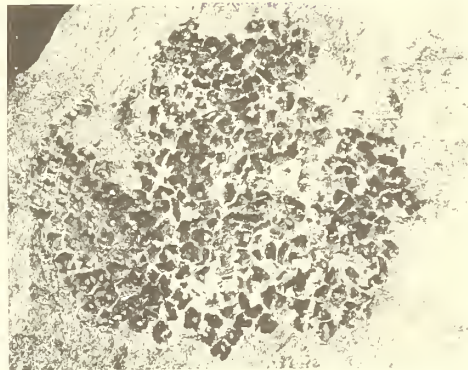
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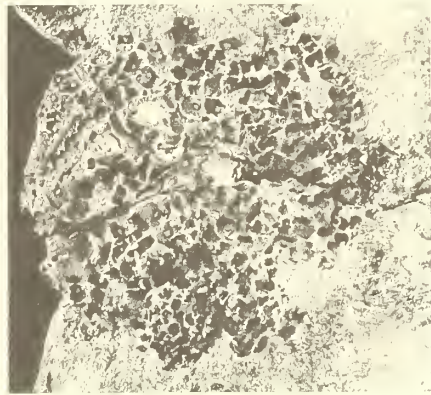
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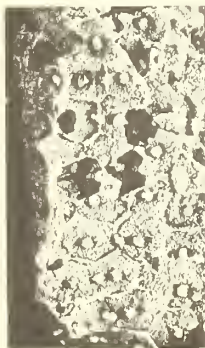
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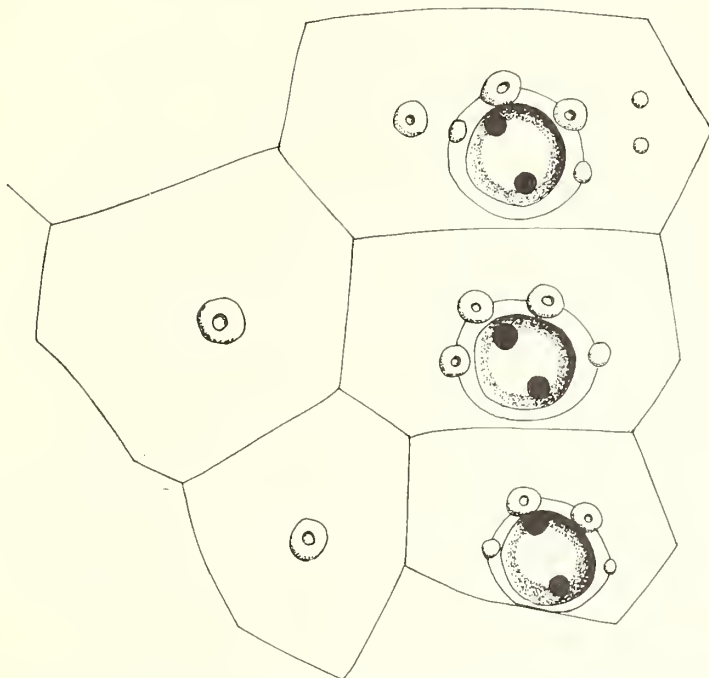


6



which two have some calcite remaining. The stereom network was the same in both types of plates.

Internal counterpart. This (2464 b. Pl. 85, fig. 4) does not correspond exactly to the external. It shows moulds of plates 2 and 3 and the pair of small plates in the central column; none of the plates of the left column; plates 3–6 of the right column; and a seventh not present on the external mould. There are no indications of a radial water



TEXT-FIG. 1. A camera lucida drawing of some of the plates of *Bothriocidaris globulus* Eichwald from Girvan.

vessel within the plates or impressed on their internal surfaces. In the perforate plates the more central pore of each pair is larger (0.3 mm.) than the other (0.2 mm.) and has an internal rim. Both pores are within a single plate.

Comparison with other species of Bothriocidaris. Only *B. globulus* Eichwald has four spine mamela on each peripodium rim. The present specimen is compared with Männil's (1962) excellent account of *B. globulus*. Männil states that the ambulacral (perforate) plates reach 4.0 mm. wide by 3.0 mm. high but the lowest are 2.0×1.5 mm. The peripodia are 1.0 mm. in diameter internally and the line joining the pairs of pores meets the vertical at $24-28^\circ$. There are two pairs of mamela on the peripodium rim, reaching 0.5 mm. in diameter, and additional mamela on the plate surface. The mamela of a pair are separated by 0.5 mm., two and three by 1.0 mm., and one and four by 1.3 mm. Männil's figure (fig. 3d, p. 169) shows four perforate mamela on the peripodia which are in the same position on a plate as those of the present specimen. The plates are strongly convex and covered with asperities.

The imperforate plates reach 3 mm. wide by 2 mm. high and bear 1–4 subcentral mamela. These plates are convex and covered with asperities.

The present specimen agrees closely with Männil's description of *B. globulus*. It differs, however, in the size of the peripodia and mamela and in not having all four mamela on the peripodium rim perforate. The similarities outweigh the differences, however, and this specimen is accepted as the seventh known example of *B. globulus*. Slight differences are to be expected in view of the widely separated localities and different stratigraphic horizon. The present specimen is from a small exposure beneath the kilns in the main quarry at Craighead, nr. Girvan (*vide* Anderson and Pringle, 1946). The Craighead Kiln Mudstones are of Uppermost Caradoc age according to Williams (1962). In Estonia, *B. globulus* occurs in the Vormsi horizon (f_{1b}) which Männil (1962) accepted as uppermost Caradoc but which Whittington and Williams (1964, p. 251) consider to be Lower Ashgill and equivalent to the Lower Drummock group of Girvan. Possibly *B. globulus* appeared earlier in Scotland than in Estonia.

B. The British Museum Specimen

These are three fragments of external mould and an internal mould of a largely disarticulated test which was probably globular and about 25 mm. in diameter (BMNH E 42523 a–d. Pl. 84, figs. 1–6, Pl. 85, figs. 9–11). A small articulated area shows rows of perforate plates and columns of imperforate plates.

E 42523 a. This counterpart shows the external mould of a small articulated area of the corona consisting of about 45 plates and measuring 15×7 mm. (Pl. 84, fig. 3, Pl. 85, fig. 10). There is also a large area of randomly orientated disarticulated plates. The imperforate plates in the articulated area are arranged in a column which apparently bends towards the bottom. (The portion of the test preserved shows neither pole. Throughout the terms 'top', 'base', etc., indicate the arbitrary orientation used for description.) The imperforate plates are hexagonal with two sides forming the top and base. The two upper sloping sides are excavated to bear part of one of a pair of pores in the adjacent perforate plates (fig. 3). The perforate plates and pore-pairs are arranged in rows at an oblique angle to the column of imperforate plates and form chevra whose axes coincide with the column of imperforate plates (fig. 2). Three relatively large plates in one row are replaced in the next, and subsequent rows, upwards by four small plates

EXPLANATION OF PLATE 85

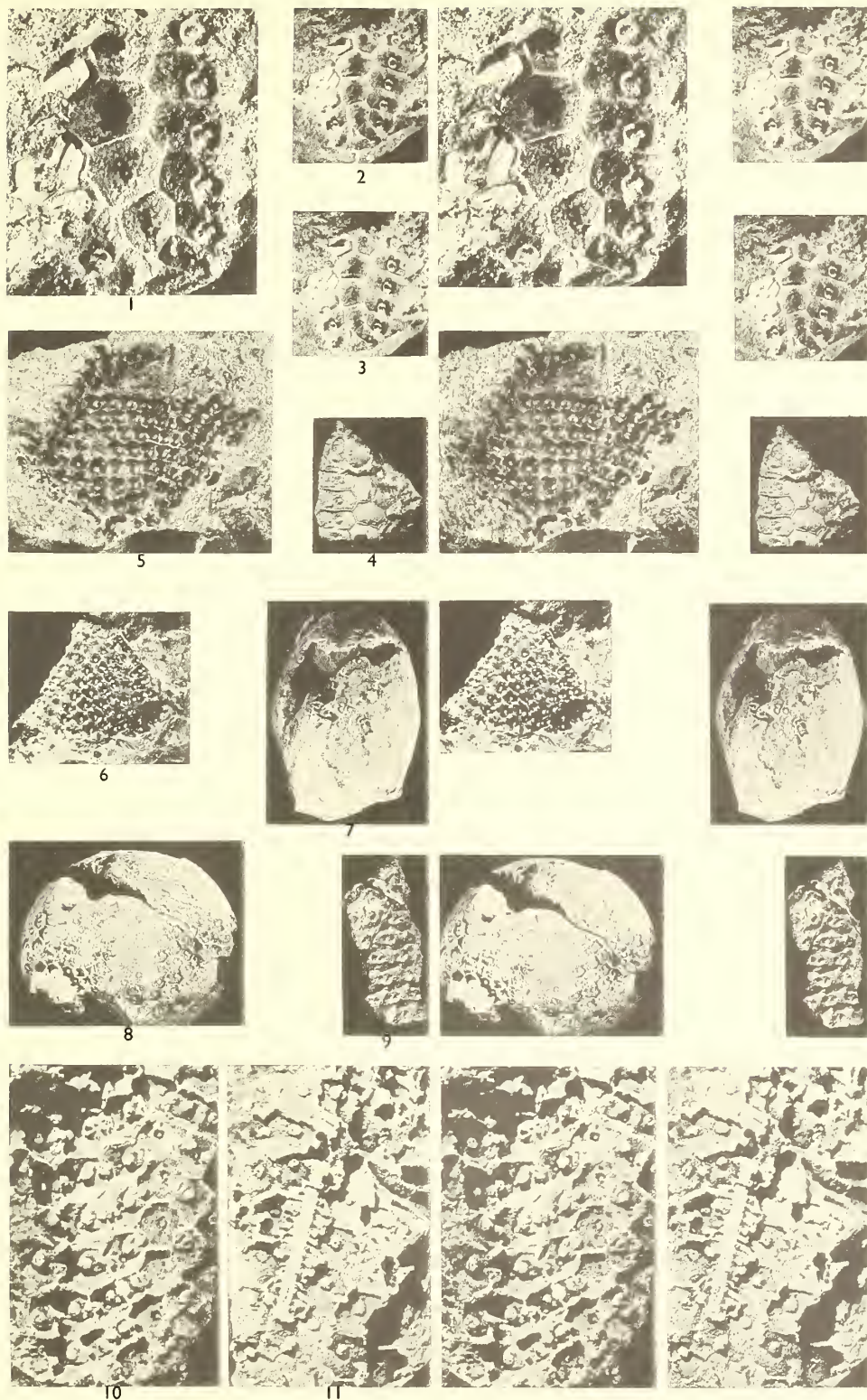
Figs. 1–4. Stereo-photos of *Bothriocidaris globulus* Eichwald from the Kiln Mudstones, Craighead, Girvan. 1, Detail of both types of coronal plates in 2464 a. 2, 2464 a. 3, A reversed pair of stereo-photos giving the illusion of reversed topography and showing the original convexity of the plates: 2464 a. 4, 2464 b internal counterpart.

Fig. 5. Stereo-photos of the holotype of *Neobothriocidaris minor* gen. et sp. nov. from the Starfish Bed, Threave Glen, Girvan.

Figs. 6–8. Stereo-photos of the paratype of *N. minor* from the Kiln Mudstones, Craighead, Girvan. 6, The external counterpart showing the arrangement of the plates. 7, 'Apical' view of the internal counterpart. 8, Lateral view of the internal counterpart.

Fig. 9–11. Stereo-photos of the holotype of *N. peculiaris*. 9, BMNH E42523 d. 10, Detail of both types of plates in BMNH E42523 a. 11, Detail of the internal counterpart of the portion of E 42523 a shown in Fig. 10, to show the casts of the radial and lateral vessels of the water vascular system. E 42523 b.

Figs. 2–9 $\times 2$, figs. 1, 10–11 $\times 5$. Figs. 4, 6–8, 10–11 whitened with ammonium chloride sublimate



of which the ones nearest the imperforate plates are smallest and apparently relatively newly formed. Spines were borne on both types of plate.

E 42523 b. The internal mould shows the exact counterpart of the area of articulated plates on *E 42523 a* and a triangular area, $14 \times 13 \times 12$ mm., adjacent to it (Pl. 84, figs. 2, 4–6, Pl. 85, fig. 11). Each perforate plate was pierced subcentrally by a pore which passed right through the plate. A second pore was shared by two adjacent plates and passed up the suture between them. Along the column of imperforate plates is the cast of a tubular vessel which gives off paired lateral branches passing within the perforate plates (Pl. 85, fig. 11). There were apparently five lateral branches for each row of perforate plates. The main vessel is 0.4 mm. in diameter and traceable for 4.5–5 mm. The lateral vessels are 0.15 mm. in diameter. One lateral vessel could be traced right across a perforate plate and was completely enclosed within it in life. The casts of the sutural pores closest to the main vessel are connected to the casts of lateral vessels in some cases. It is difficult to interpret this structure as anything other than a radial vessel of the water vascular system giving off lateral branches to feed the pore-pairs and tube-feet. The number of lateral branches suggests there were five perforate plates in each row on either side of the columns of imperforate plates and therefore there were ten perforate plates between adjacent columns.

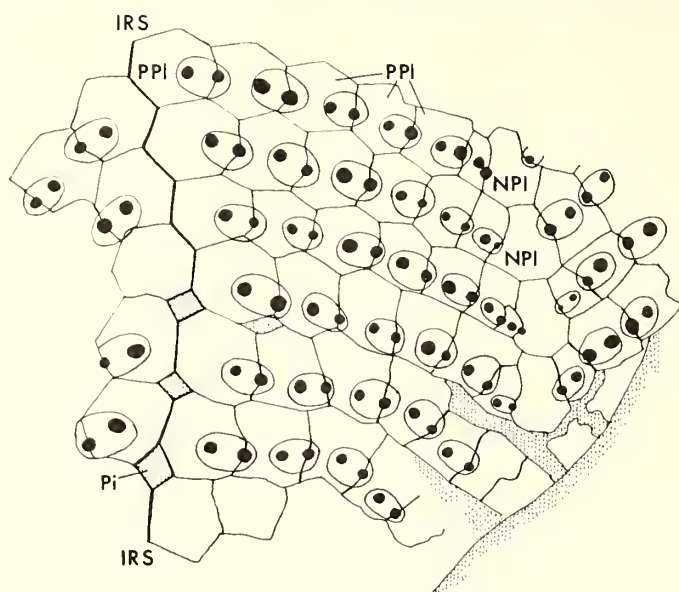
The triangular area is bounded on the right by five imperforate plates of another column showing another radial water vessel. The left margin is confluent with the area described above. Thus this counterpart shows an area between two radii of the test apparently somewhere near the ambitus as the two radii converge only slightly upwards. In this region there are nine perforate plates in the rows between the two radii. In one row there is a small accessory plate which bears no pores. Despite the odd number of plates in the rows between the radii there is no central inter-radial column of perforate plates which can be distinguished from the others. The two limbs of adjacent chevrons alternate and there is a single suture, the inter-radial suture, running down the test which has no sutural pores (text-fig. 2). All other vertical sutures have sutural pores. The perforate plates adjacent to the inter-radial suture are noticeably larger than those adjacent to the columns of imperforate plates. There is a gradual increase in size in an ad-inter-radial direction.

The radial and lateral vessels of the second radius are the same size as those of the first. Each of the five imperforate plates is 1.2–1.3 mm. vertically.

A small portion of this mould has *E 42523 c* as external counterpart. The latter shows part of another column of imperforate plates but no corresponding radial water vessel is preserved on *E 42523 b*. Several of the perforate plates have complete casts of the central pores preserved. There was no connection between them and the lateral water vessels.

E 42523 c. This is an external mould of a small area of articulated plates corresponding to part of *E 42523 b* (Pl. 84, fig. 1). It shows the five plates of the right radius of *E 42523 b*, one of which is slightly out of line so there can be no doubt as to which plates correspond on the internal and external counterparts. In many moulds of perforate plates small portions of the casts of the lateral vessels can be seen attached to casts of the sutural pores. There is another column of imperforate plates which apparently terminates or is interrupted.

E 42523 d. This is an external mould of a very small area of articulated plates corresponding to part of *E 42523 b* (Pl. 85, fig. 9). It shows the plates adjacent to the inter-radial suture and the small accessory plate without pores which bore spines. There are marked pits at the junction of three sutures along the inter-radial suture.



TEXT-FIG. 2. A camera lucida drawing of part of the test of HM E 1247 to show the arrangement of poriferous plates (PPI) in rows and non-poriferous plates (NPI) in a column. IRS, inter-radial suture; Pi, pits.

The imperforate plates are basically hexagonal, approximately 1.4 mm. high and wide, and of unknown thickness. Each plate has two sides adjacent to imperforate plates above and below and is in contact with four perforate plates laterally (text-fig. 3). The two upper sloping sides bear half a sutural pore and the surface is slightly excavated to form part of the peripodium. The peripodium rim is less conspicuous in this area than at the opposite end. Centrally in each plate there is an elongate spindle-shaped elevation, 0.85 mm. long, consisting of a large central perforate mamelon 0.35 mm. in diameter, and two secondary mamela, one above and one below. The upper mamelon is generally larger, reaching 0.27 mm. and frequently perforate. The lower rarely exceeds 0.20 mm. and is imperforate.

The smallest perforate plate is 0.6 × 0.6 mm and is trapezoid with the shortest side adjacent to an imperforate plate. In the same row of perforate plates one plate near the inter-radial suture measures 1.5 × 1.5 mm. Not all the large plates are adjacent to the inter-radial suture, however. One plate adjacent to an imperforate plate measures 1.6 × 1.3 mm. but is replaced by two small plates in the next row.

Perforate plates adjacent to imperforate plates have their lower sloping sides excavated to bear the other half of the common sutural pore (text-fig. 3). Subcentrally there is

another pore opening externally at the same level as the sutural pore and provided with a rim on the internal surface. The pores vary in diameter from 0.13 mm. in the smallest plates to 0.25 mm. in the largest. They reach 0.3 mm. internally. They are set at the base of an oval peripodium which varies from 0.66×0.4 mm. in the smallest plates to 0.8×0.6 mm. in the plates near the inter-radial suture. The increase in size of the pore-pairs is much less than that of the plates bearing them. The two pores are separated by a slight ridge (not developed in the smaller peripodia) on the peripodium floor. The peripodia have a continuous rim, more strongly developed near the single perforate mamelon. The smallest plates lack mamela as they are only 0.1 mm. larger than the peripodia. The largest plates have two additional mamela about 0.5 mm. apart. These can be distinguished as a larger, 0.25 mm. diameter, set 0.3 mm. from the primary mamelon which reaches 0.3 mm.; and a smaller below, 0.16 mm. diameter, set 0.43 mm. from the primary. There are also slight swellings on the peripodium rim either above or below the primary mamelon which may have been secondary mamela (E 42523 c).

On the far margin of the perforate plates there is another excavation for half a sutural pore and this arrangement continues to the inter-radial suture. Although the pore pairs are unequally shared by two plates, the peripodium forms a complete unit and strongly resembles those of *Bothriocidaris pahleni* Schmidt and *B. globulus* Eichwald, specimens of which were available for comparison.

C. The Hunterian Museum Specimen

Plate 85, fig. 5

This is an external mould, 18×15 mm., of part of a test (HM E 1247). The major part is still articulated and shows one radius, considerable areas of adjacent 'inter-radii', and one inter-radial suture. The numbers of plates between the radius and inter-radial suture in five rows are 5, 6, 7, 6, 6 (text-fig. 2). In the second and third rows the plates adjacent to the radius are very small, 0.3×0.5 mm., and incompletely developed. The column of imperforate plates bends slightly towards one pole. The area beyond the termination is partly disarticulated. A short distance from the termination there are two plates without pores which may belong to the apical system. If so, the chevra were inverted in life. In this specimen perforate plates developed along the margins of the imperforate plates and there were two which were still forming when the animal died. The inter-radial suture shows some external pits and there were small depressions on the perforate plates adjacent to it. Several plates show casts of lateral water vessels.

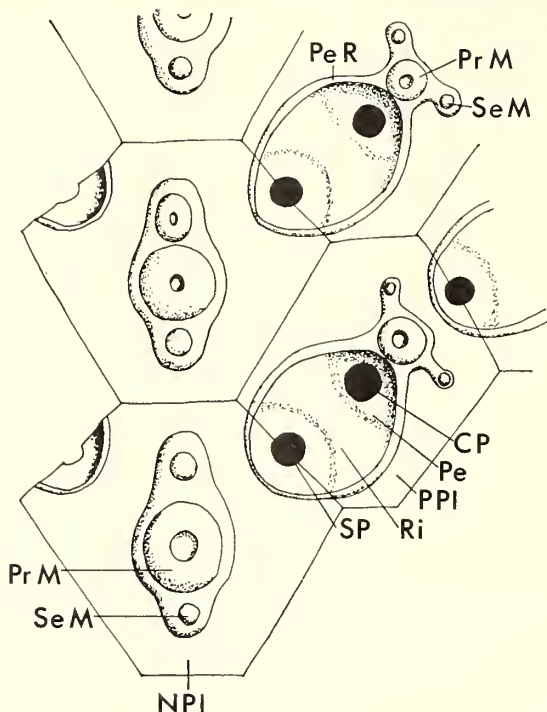
There are only two mamela on the imperforate plates: a large central perforate mamelon and a smaller imperforate one, corresponding to the larger of the two on the previous specimen (text-fig. 4). The peripodium rims are less distinct and occasionally impinge on a third plate. On the rim there is a large perforate mamelon and a single imperforate mamelon adjacent to it. Also adjacent to the primary mamelon is a small pit in the plate surface. Occasionally there is a single swelling on the rim below the primary mamelon (text-fig. 4).

The largest perforate plate is 1.25×1.25 mm. with mamela 0.35 and 0.23 mm. in diameter. The central pores reach 0.23 mm. The mamela of the imperforate plates are 0.33 and 0.27 mm. and the plates reach 1.05×1.25 mm.

D. The Lund Specimen

Plate 85, figs. 6-8

These are four fragments of external mould and an almost complete internal mould. All the fragments of external mould are coated with a dark brown deposit which obscures the finer detail. Only one fragment shows the plate arrangement clearly.



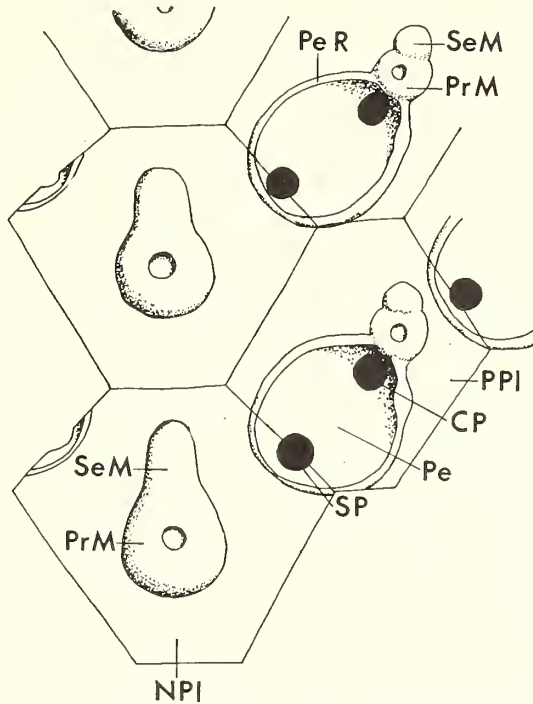
TEXT-FIG. 3. A sketch of the ornament of the plates of BMNH E 42523. CP, central pore; NPI, non-poriferous plates; Pe, peripodium; PeR, peripodium rim; PPI, poriferous plates; PrM, primary spine mamelon; Ri, ridge; SeM, secondary spine mamelon. Figs. 3 and 4 are in this orientation for ready comparison with the plates of *Bothriocidarid*. It is quite possible, however, that Figs. 2-4 and 6 are inverted.

The internal mould. This is almost complete but the surface is worn, obscuring some details. It is slightly compressed and measures 15×10 mm., with a height of 11 mm. Five columns of imperforate plates and five inter-radial sutures could be detected after coating with ammonium chloride sublimate. They converge towards the top of the mould. Unfortunately this region is worn and no details can be distinguished. There is no indication of a large aperture, such as the peristome, and this may be the apical region. If so, the chevra were inverted in life. At the opposite pole the matrix still obscures the plates so neither peristome nor apical system can be recognized definitely.

There are regularly four perforate plates in each row and thus any two adjacent radii are separated by eight perforate plates. Occasionally accessory plates without pores appear near the inter-radial sutures. The maximum number of imperforate plates

distinguished in a column was seven. The maximum diameter of these plates averages 1.0 mm. In two cases fragmentary casts of radial water vessels have been preserved. The perforate plates reach 1.35 mm. and the arrangement of the pore-pairs is as in the two previous specimens.

The external mould (Pl. 85, fig. 6). Only one fragment is well preserved and shows one radius with seven or eight imperforate plates and one inter-radial suture. Both approximate towards one edge of the mould which was near a pole. Near the position of the



TEXT-FIG. 4. A sketch of the ornament of the plates of HM E 1247.
Symbols as in text-fig. 3.

pole there are two large imperforate plates, one measuring 1.35×1.0 mm. and bearing three large mamela. These two plates may have been part of the apical system but as the column of imperforate plates terminates before reaching them this seems unlikely. In addition the chevra are the right way up in this orientation which contradicts the evidence of the internal mould.

Near the pole the inter-radial suture follows a zigzag course with perforate plates alternating on either side. Near the ambitus the perforate plates are opposite each other and four sutures meet in a distinct pit in the external surface. The inter-radial suture has become an almost straight line. Each pore-pair consists of a sutural, and a central, pore opening in a rimmed peripodium. The rim bears one perforate mamelon adjacent to which is a smaller imperforate mamelon. Below these is a marked pit in the plate surface. The imperforate plates have a central perforate mamelon and one appears to have a single secondary mamelon but the details are obscured by the brown deposit.

E. The Lamont Specimen

This specimen was briefly examined before it was returned to Dr. Lamont. It is an internal mould showing a large area of articulated plates but neither pole. It adds nothing new to the description of these specimens. In one row of perforate plates each plate has one less lateral vessel passing through it than the immediately ad-radial plate, thus confirming the reconstruction of the water vascular system given in text-fig. 6.

AFFINITIES OF THE SPECIMENS

Assuming the latter four specimens were congeneric this genus is characterized by five single columns of imperforate plates; perforate plates arranged in rows forming chevra; pore pairs set in a deep peripodium with a perforate mamelon on its rim; one pore of each pore-pair shared by two plates.

As far as the present writer is aware there are only three genera of Palaeozoic echinoids with single columns of imperforate plates. These are *Bothriocidaris* Eichwald 1860, *Cravenechinus* Hawkins 1946, and *Xenechinus* Kier 1958. The Girvan specimens resemble the latter two genera, which together form the Cravenechinidae, in having many plates between columns of imperforate plates. In the Cravenechinidae the perforate plates are arranged in columns (eight in *Cravenechinus* and four in *Xenechinus*) not rows, and each pair of pores is entirely within one plate. *Xenechinus* has radial water vessels covered internally by a calcitic deposit and lateral vessels in shallow grooves (Kier 1958, 1965). Superficially this resembles the condition in the BMNH specimen but in *Xenechinus* the radial water vessels are beneath the radial sutures and the single columns of imperforate plates are inter-radial. This was probably the case in *Cravenechinus* also but the internal surface is unknown.

The Girvan specimens resemble *Bothriocidaris* in having pore-pairs set in peripodia with spine mamela on the peripodium rims. They differ, however, in the arrangement and number of the perforate plates and in having one pore of each pore-pair shared by two plates. The positions of the radial water vessels in the BMNH specimen and *Xenechinus* prevents assigning the Girvan material to the Cravenechinidae. The strong resemblance between the pore-pairs and peripodia of the Girvan specimens and *Bothriocidaris*, however, suggests they are closely related.

Männil (1962) has accepted four species of *Bothriocidaris* separated on the details of the peripodium rim. The BMNH specimen has one large primary mamelon on the peripodium rim and two smaller mamela on the plate surface (text-fig. 3). The imperforate plates have one large perforate mamelon and two smaller mamela, one above and one below. The Hunterian specimen has one primary and one secondary mamelon on both types of plate (text-fig. 4).

Apart from these differences the peripodium rim is less distinct and occasionally shared by three plates; the peripodium is deeper and the pores nearer the margins on the Hunterian specimen than on the BMNH specimen. The plates of the Hunterian specimen are smaller and there are more of them in a row suggesting their small size is not a feature of growth. These two specimens are considered to belong to separate species.

SYSTEMATIC PALAEOLOGY

Family Bothriocidaridae Klem 1904

Diagnosis. A family of regular echinoids with single columns of imperforate plates; with pore-pairs opening externally in distinct peripodia surrounded by a rim on which perforate spine mamela are developed.

Genus *Neobothriocidaris* nov.

Type species. *N. peculiaris* gen. et sp. nov.

Diagnosis. A genus of Bothriocidaridae with single radial columns of imperforate plates; with perforate plates arranged in rows forming chevra with their axes coincident with the radial columns; with one pore of each pore-pair shared by two adjacent plates.

Regional distribution. Craighead Inlier, Girvan, Ayrshire.

Stratigraphic Range. Ordovician. Craighead Kiln Mudstones (Upper Caradoc) to Starfish Bed (Middle or Upper Ashgill).

N. peculiaris gen. et sp. nov.

Holotype. BMNH E 42523 a-d.

Type locality. Locality 7 (Lamont, 1935), Threave Glen, Girvan.

Type Stratum. Starfish Bed, Upper Drummock Group. According to Ingham (1966, p. 495) this is on the boundary of the Middle and Upper Ashgill. *N. peculiaris* is only known from the type locality.

Diagnosis. A species of *Neobothriocidaris* with one primary and two secondary spine mamela on the imperforate plates; with one primary mamelon on the peripodium rim; and two secondary mamela on the plate surface of the perforate plates.

N. minor gen. et sp. nov.

Holotype. HM E 1427.

Type locality and stratum as for *N. peculiaris*.

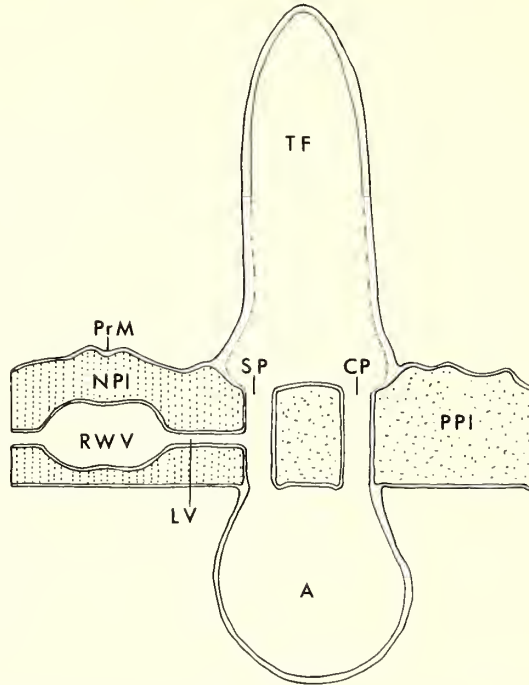
Diagnosis. A species of *Neobothriocidaris* with one primary and one secondary spine mamelon on the imperforate plates; with one primary mamelon on the peripodium rim; and one secondary mamelon on the plate surface of the perforate plates.

N. minor (the Lund specimen) is recorded from the Craighead Kiln Mudstones, below the kilns at Craighead Quarry, Girvan, as well as from the type locality.

The full complement of mamela is only developed on large perforate plates of which those adjacent to the inter-radial suture are taken as typical. Lamont's specimen cannot yet be assigned to either species above. It is from the Starfish Bed.

RECONSTRUCTION OF THE WATER VASCULAR SYSTEM IN
NEOBOTHRIOCIDARIS

It is assumed that the madreporite in *Neobothriocidaris* gave rise to a stone canal leading to a circumoesophageal ring canal off which five radial water vessels arose, as in all other sea urchins. The radial vessels may have been partly or completely within the coronal plates. This was the case in at least two radii of the BMNH specimen as is



TEXT-FIG. 5. Reconstructed transverse section through a radial water vessel (RWV) and a tube-foot (TF) of *Neobothriocidaris* gen. nov. showing a lateral vessel (LV) feeding the sutural pore (SP) within the plate of the corona. A, ampulla; CP, central pore; PPI, poriferous plate; PPI, poriferous plate; PrM, primary spine mamelon.

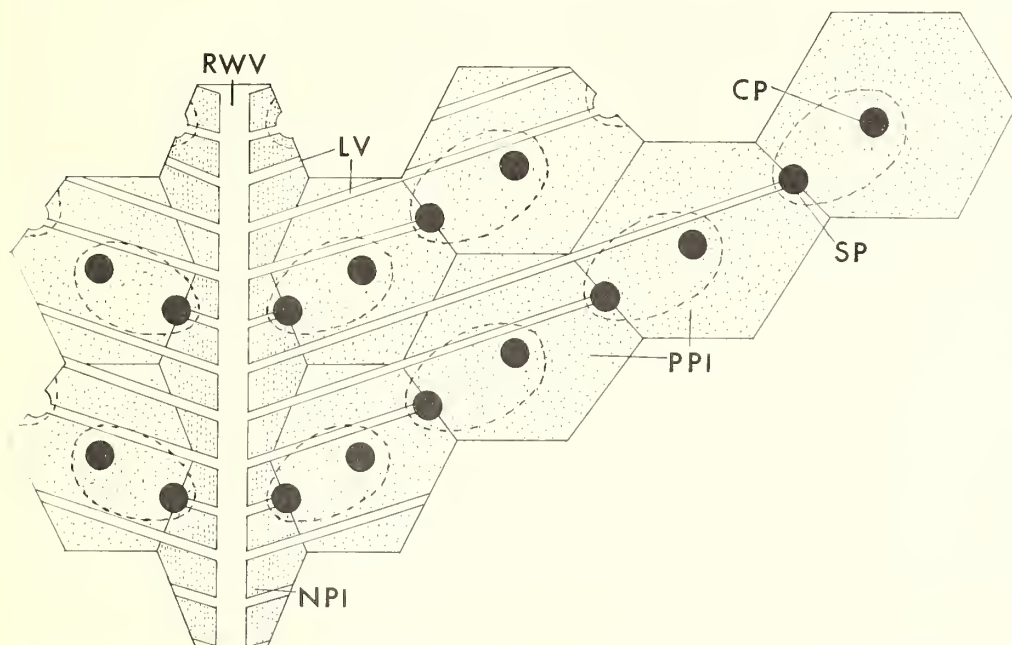
shown by the casts seen on E 42523 b. There was no evidence of the radial vessel of the third radius however nor in the majority of plates in the five radii of the Lund specimen. If the radial vessels were entirely within the coronal plates in life casts would be formed only when the covering was damaged after death. The radial vessels were probably within the plates since the casts of the lateral vessels are in the BMNH and Hunterian specimens. Casts of radial vessels are only preserved in the Lund specimen where the plates are slightly damaged. Text-fig. 5 shows the interpretation adopted here.

In plan view (text-fig. 6) the perforate plates are arranged in chevra with their axes coincident with the radial column of imperforate plates. In all cases the lateral vessels are also arranged in chevra at a slightly greater angle to the radial line. This arrangement

allows lateral vessels to feed tube-feet in perforate plates not adjacent to the column of imperforate plates, and is preserved in Lamont's specimen.

RE-INTERPRETATION OF BOTHRIOCIDARIS

The internal mould of *Neobothriocidaris peculiaris* gen. et sp. nov. (BMNH E 42523 b) has casts of radial and lateral water vessels preserved. By definition the plates bearing radial water vessels are radial in position but in this specimen they are imperforate



TEXT-FIG. 6. Diagrammatic reconstruction of part of the water vascular system of *Neobothriocidaris* gen. nov. CP, central pore; LV, lateral vessel; NPI, non-poriferous plates; PPI, poriferous plates; RWV, radial water vessel; SP, sutural pore.

plates which have previously been regarded as inter-radial in *Bothriocidaris*. Assuming *Neobothriocidaris* and *Bothriocidaris* are closely related it seems advisable to reinterpret the latter with the imperforate plates radial. Lack of knowledge of the apical system and peristome in *Neobothriocidaris* unfortunately prevents a complete comparison. The main effect of the proposed re-interpretation is that all radial features became inter-radial and vice versa. To reduce confusion in the following account radial and inter-radial are italicized when referring to the re-interpretation.

The Apical System. The apical system of *Bothriocidaris* is unique in lacking genital and terminal pores and in consisting of five, not ten plates. The five plates were regarded as radial and therefore as ocular plates, one of which was modified as a madreporite. These plates now become *inter-radial*, genital plates with one a madreporite, as in later echinoids. The madreporite is used to orientate the test and lies in inter-radius 2. It is assumed this was the case in *Bothriocidaris*. Where were the oculars if the apical plates

were genitals? The key to this may lie in the growth of the corona which is intimately associated with these plates in later echinoids.

The Corona. Jackson (1912, p. 35) showed that in normal echinoids addition of new coronal plates is limited to the exterior margins of the oculars. Along these five 'placogenous zones' new plates appear for both radial and inter-radial columns. In a corona formed of ten pairs of columns of plates there are two ways of combining the columns into symmetrical sets of four, i.e. with an inter-radial or a per-radial suture central. In *Bothriocidaris* there are only fifteen columns of plates which can only be arranged in symmetrical sets of three in one way, i.e. with the single columns of imperforate plates central. Unless placogenesis occurred in a different way in *Bothriocidaris* one would expect it to have centred on the spaces between the apical plates which would be regarded as genitals.

If oculars occur in *Bothriocidaris* they would be between the apical plates. The small plates within the apical system cannot be oculars as they are often completely enclosed within the ring of genitals. The topmost plates in the *radial* columns are often apparently newly formed and also cannot be oculars.

Jackson (1912) showed that echinoids with an abnormal number of ambulacra and inter-ambulacra either had a corresponding abnormal number of oculars or, if five oculars were present, the terminal pore was absent in the ocular associated with the missing ambulacrum. It is not certain whether the entire radial water vessel or only the terminal portion was absent in these cases but placogenesis seems to be associated with the terminal portions of the radial vessels in normal echinoids. In *Bothriocidaris* placogenesis probably took place at the margin of the apical system between the apical plates. In *Neobothriocidaris* this stage of growth was followed by a stage where additional perforate plates were added along the entire length of the columns of imperforate plates, each imperforate plate giving rise to a row of perforate plates on either side. The occasional extra imperforate plates of *Bothriocidaris* may have arisen in this way also but this is not certain.

If the entire column had the ability to stimulate placogenesis, then perhaps the column as a whole is the homologue of an ocular plate in later echinoids. It is suggested here that the corona of *Bothriocidaris* is formed of five ambulacral groups consisting of a central *per-radial* column of imperforate plates and two lateral *ad-radial* columns of perforate plates, together forming the homologue of a normal ambulacrum. Apparently the only truly *inter-radial* feature of the corona is the *inter-radial* suture between adjacent ambulacral groups. To develop a normal echinoid corona from *Bothriocidaris* it would be necessary to reduce the *per-radial* columns to five single ocular plates, unite the *ad-radial* columns to form normal ambulacra, and develop normal inter-ambulacra.

The Peristome. Under the conventional interpretation the primordial ambulacral plates of *Bothriocidaris* obey Lovén's Law. Lovén's Law states that the primordial ambulacral plates of columns Ia, IIa, IIIb, IVa, and Vb are larger than those of columns Ib, IIB, IIIa, IVb, and Va. The numbering is according to Lovén's system (Lovén, 1874, p. 13) with the madreporite in inter-radius 2. If *Bothriocidaris* is orientated in this way under the present interpretation the primordial ambulacral plates do not obey Lovén's Law or, perhaps more correctly, they do but they are one plate out all round the peristome. Durham and Melville (1958, p. 176) pointed out that in a pair of columns of alternating

plates the basal plate in one column must be larger than that of the other column, if the bases are level, for purely spatial reasons. It is not known why all five ambulacra should follow Lovén's Law but the reason for one plate (in each pair of columns) being larger is obvious. This does not arise in the inter-ambulacra of later echinoids as they terminate in a single plate. In *Bothriocidaris* the ambulacral groups consist of three columns, the lateral pair being symmetrically disposed about the central *per-radial* column. The only alternation of ambulacral plates, essential for Lovén's Law, is about the *inter-radial* suture. The two primordial ambulacral plates of one ambulacral group tend to be the same size as they are symmetrically developed on either side of the adoral *per-radial* plate. However, one of the primordial ambulacral plates on either side of an *inter-radial* suture must be larger. If these plates are to obey Lovén's Law purely spatial reasons will pair them about the *inter-radial* suture. In later echinoids the pairing is obvious as each pair is separated by a single interambulacral plate. In *Bothriocidaris* the ten primordial ambulacral plates form a closed circlet and may be paired in two ways. Irrespective of interpretation, for Lovén's Law to occur, the pairing must be about the zigzag *inter-radial* suture. The fact that the primordial ambulacral plates of *Bothriocidaris* obey Lovén's Law but are one plate out, as opposed to being three or five plates out, suggests that the arrangement is as close as is mechanically possible to that of later echinoids.

Recently Durham (1966) has thrown doubt on the interpretation of the plates around the peristome. Männil (1962) described ten unpaired imperforate plates adoral to, and firmly sutured to, the primordial ambulacral plates. Durham related these plates to the buccal plates of the larval *Psammechinus miliaris*. In this species the buccal plates are paired inter-radially prior to metamorphosis and radially subsequently. A single tube-foot appears first in Ib, IIb, IIIa, IVb, and Va subsequent to metamorphosis. The ten plates adoral to the primordial ambulacral plates of *Bothriocidaris* are unpaired, imperforate and regularly alternate large and small. The present writer prefers to accept these as basi-coronal plates without known homologues in later echinoids and continues to accept the ten adoral perforate plates as primordial ambulacral plates. If Durham's (1966) suggestion is accepted, however, the primordial ambulacral plates of *Bothriocidaris* do not obey Lovén's Law since they are unpaired.

The peristomial opening of *Bothriocidaris eichwaldi* Männil is pentagonal (Männil, 1962). The angles of the pentagon are *inter-radial* and in Recent echinoids these angles correspond to the points of emergence of the teeth. If this were so in *Bothriocidaris* the teeth were *inter-radial* (as in recent echinoids) under the new interpretation. Unfortunately Männil located teeth in *B. eichwaldi* which were inter-radial under the conventional interpretation. These teeth are unlike those of later echinoids and none was located in the specimen showing the entire jaw apparatus.

The Jaw Apparatus. The jaw apparatus of *B. eichwaldi* is composed of the following elements:

1. A conical 'central formation' of five 'inter-radially situated double sectors' (Männil, 1962).
2. 'Jaws', ten paired inter-radially.
3. 'Drumsticks', ten paired radially.
4. 'Distal plates', five (only one seen) radial.

For the present interpretation it is necessary to read *radial* for inter-radial and vice versa. Under either interpretation it is difficult to homologize these structures with a typical Aristotle's Lantern and Männil seems deliberately to have avoided using terms implying homologies. He did however suggest the following homologies:

- 'Jaws' = Pyramids
- 'Drumsticks' = Epiphyses
- 'Distal plates' = Rotulae

Durham (1966) has interpreted Männil's evidence to give a structure more closely related to an Aristotle's Lantern. He regarded the 'central formation' as being five unpaired inter-radial teeth, and the 'Jaws' and 'Drumsticks' together as forming the pyramids (see Durham, 1966, fig. 5, p. 375). If this interpretation is correct then the jaw apparatus of *Bothriocidaris* is more easily related to that of later echinoids under the conventional, than under the new, interpretation.

CONCLUSIONS

It is unfortunate that the apical and peristomial regions of the test of *Neobothriocidaris* are unknown and cannot be compared with those of *Bothriocidaris*. The proposed reinterpretation of *Bothriocidaris* is tentative and offered as a possible alternative to the previous interpretation. Durham (1966, p. 375) states: 'The most unorthodox features of the test of *Bothriocidaris* are the radial position (in one of the oculars) of the madreporite, the absence of recognizable genital plates, and the single-columned inter-ambulacra that do not extend to the peristomial margin.' It is thought that all these features can be more easily understood under the new interpretation. The madreporite is inter-radial in a genital plate, homologues of oculars can be suggested, and the complex mode of coronal growth described by Durham (1966) becomes unnecessary.

At the present state of knowledge the new interpretation raises as many questions as it solves. On the whole the apical region fits better into the new interpretation than the old but the peristomial region and jaw apparatus fit the old interpretation better. Which is the more important cannot yet be settled. Ever since its first description over a century ago *Bothriocidaris* has puzzled palaeontologists. Despite new information gained in recent years it remains as enigmatic as ever or possibly even more so.

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TERTIARY HOMOPTERA OF STAVROPOL AND A METHOD OF RECONSTRUCTION OF CONTINENTAL PALAEOBIOCOENOSES

by E. E. BEKKER-MIGDISOVA

ABSTRACT. The fossil remains of insects from Vishnevaya Balka are the principal basis for studies of the entomofauna of the Caucasus in the Miocene period. The representatives of the Homoptera (monophagous and oligophagous) which are closely associated with certain genera and species of plants, have been carefully studied. The wealth of species of Psyllidea (mainly monophagous) allows us on the basis of biocoenotic relationships to enlarge the list of plants existing in the Stavropol region in Karagan times.

The geological section of Vishnevaya Balka comprises a considerable portion of the Karagan horizon from above the Chockrack boundary. It shows some regularity in the burials of the representatives of different orders of insects by layers. Diptera recorded in the lower layers as only 17%, rise to 48% in the upper layers. Homoptera dominate in the lower layers, with 35%. The beetles and Hymenoptera make up no more than 3-10%; Trichoptera 15-24%, falling in the upper layer I to 7-8%. The biocoenotic relationships of Homoptera and Diptera enable us to estimate the changes of biocoenoses in time. During the deposition of the lower layers a woody vegetation (trees and shrubs) prevailed while herbaceous vegetation was characteristic of the upper layers, pointing to the gradual steppization of the area.

IN 1939 a large collection of fossil insects (3,600 specimens) was found near the town of Stavropol. They were obtained from the Karagan strata (the Middle Miocene of the Caucasus). A detailed study of the Miocene entomofauna and the description of the locality Vishnevaya Balka enable us to define the environmental conditions of biocoenoses and to trace their modifications during that geological period. This paper is an extension of the discussion included in my earlier paper (1964); it considers a new method of reconstructing palaeobiocoenoses using the 'Principle of Actualism' and citing many examples of the ecology of different orders of modern insects.

The insects are the most numerous class of animals and the representatives of different groups are adapted to diverse environmental conditions. Among them are phytophagous insects feeding on some certain food plants, as monophagous and oligophagous species; predators and parasites each adapted to its respective species or groups of animals, either vertebrates or invertebrates.

The Homoptera are a group of suctorial plant-feeding insects closely connected with their host-plants. Metcalf (1946) has pointed out that most of the species in the Homoptera are limited to a single or a narrow range of host-plants. This characteristic feature together with their insufficient powers of flight makes them very valuable as geographical indices. Their food associations being constant, changing of the host usually leads to morphological modifications and the emergence of new forms. Among Homoptera, Psyllidea are generally monophagous. Aphidea change their host during a season, either from a woody plant to a herbaceous one, or from one woody plant to another. As a rule these host-plants are of a quite definite genus and species. With the loss of one of the two hosts, heterocyclic species became anholocyclic leading only to parthenogenous generations of apterae (pseudohiemosistens or pseudofundatrix) and alatae (alata exsulans or alata non migrans).

Most of the psyllids described belong to recent forms whose host-plants are well known. In such cases we may confidently say that in that locality there were in existence plants of the same genus and closely related in species to the modern representatives. In other cases some new species of psyllids closely related to modern forms are found as well; so we may suppose that they might have inhabited some plants closely related to the modern representatives of the same or a related genus of the same family.

The study of phytophagous Homoptera (monophagous and oligophagous) enables us to make up a preliminary list of plants which were probably included in the phyto-coenoses of the Stavropol region in Karagan times. Generally it comprises all the species which were identified by Palibin (1936) for that locality. Only in a few cases were there plants unknown for the Stavropol region of Karagan times, but found in the Chockrack strata of the Caucasus, or plants belonging to genera which are at present found in the Caucasus. The latter are perhaps of the Caucasus-Middle Asia, or of Asia Minor origin. Consequently the representatives of those genera might have existed there from the Tertiary period. The list given above has been partly confirmed by the data of spore-pollen analysis (Grossheim and Gladkova 1950).

The collections of insects from Vishnevaya Balka serve now as the basis for the understanding of the Caucasus Miocene entomofauna. Water insects, plant feeders, and saprophages, form the greater part of entomofauna making up almost equal groups; predators and parasites occur in lesser number (Rohdendorf 1939).

Among the Homoptera studied the groups inhabiting woody plants prevail. From 30 species and over 300 specimens of psyllids only 3 specimens (belonging to 3 species) inhabited herbaceous plants. The fact that only a few leaf-hoppers, the inhabitants of herbaceous vegetation of moist meadows and flood plains (*Cicadella viridis* L., *Eupteryx*, *Paramesus*), were found, confirms the insufficient development of those phytocoenoses. On the other hand among Diptera the inhabitants of herbaceous vegetation (Chloropidea) occur together with those of deciduous forests and shrubs (Sciaridae and Agromyzidae).

The geological section of Vishnevaya Balka comprises a considerable portion of the Karagan horizon above the Chockrack boundary. Throughout the section the fossil insect remains occur in the interlayers of the same fine-grained marl. The insects studied are of similar small to medium size. The phenomenon of taphonomic character such as a size selection of insects in the marly interlayers, cannot influence considerably the quantity of the representatives of separate orders. The burials of the relatively large Trichoptera are consistent throughout the marly interlayers of the whole section, while small psyllids prevail in the lower layers and Diptera (including also small forms) in the upper layers. All this enables us on the basis of the number and variety of fossil remains to speak about the changes in the composition of the entomofauna in the course of the deposition of the sediments and to estimate the changes in the composition of respective plant associations.

In the entomofaunal assemblage Coleoptera and Hymenoptera are almost constant in number in all layers at about 3–10%; Trichoptera vary from 15 to 24% with the exception of layer I where they are reduced to 7–8%. It is quite different with Diptera and Homoptera. Diptera increase to 17–24% in the upper layers (XVI–X), amounting to 30% in layer V, to 33% in layer I and even to 48% in exposure 4 which is the slide of several layers in the geological section of Vishnevaya Balka; it is situated above layer I. Thus in the upper layers Diptera become a dominant group.

On the contrary Homoptera dominate in the lower layers (layer XVI), making up about 35%. They are present in various assemblages where willow and rosaceous groups of psyllids prevail. There occur also single representatives of psyllids from high cranberry (*Viburnum*), *Caragana* or acacia, cinnamon, and pistachio (*Pistacia*). The whole composition of Homoptera fauna points to the existence of woody vegetation. In layer XI the number of Homoptera sharply decreases, falling as low as 8–10%, and of the whole rich psyllid assemblage only two species feeding on Leguminosae are left, one from *Caragana* or acacia, the other from lucerne (*Medicago*). In layer IX Homoptera increase, and again groups of willow and rosaceous psyllids appear but with smaller number of species. Separate representatives of psyllids from high cranberry (*Viburnum*), *Astragalus*, *Elaeagnus*, and two species from *Ulmus* are also found. In the upper layers (VIII, V, III) and exposure 4, Homoptera make up no more than 3–5%; only in layer I do their numbers rise to 16%, but consist almost exclusively of Aphididea. In the upper layers (exposure 4) side by side with numerous psyllids from legumes and aphids, small cicades (plant-hoppers, frog-hoppers, and leaf-hoppers) are found.

The above analysis shows a change of biocoenoses in the course of the Karagan strata formation conditioned by one or another kind of plant association. In the lower layers insects connected with arborescent plant associations prevail while in the upper layers insects related to herbaceous plants dominate. It is possible that during the period of the Upper Karagan strata formation herbaceous vegetation developed sufficiently and that forest plant associations were replaced by those of steppe character.

Summing up the material on the composition of entomofauna and flora we appear to have contradictory data. On the one hand there occur the inhabitants of arid areas, psyllids from *Astragalus*, *Valerianella*, and *Pistacia*, and also psyllids from *Medicago*. The latter plant, owing to its long roots (about 3 m.), can grow in relatively arid areas. The existence also of evergreen plants is confirmed by the presence of fossil remains, and by the burial of psyllids inhabiting those plants in Karagan times.

On the other hand there are indications of the existence of deciduous forests in the occurrence of Sciaridae (Diptera) whose larvae live in leaf litter and are associated with the formation of humus. The presence of Agromyzidae whose larvae mine leaves shows that there was an abundance of angiospermous plants, mainly trees and shrubs and partly herbaceous vegetation.

Finally there is evidence of the existence of wet meadows with herbaceous vegetation. For instance there are the remains of Tipulidae (Diptera) and a leaf-hopper (*Cicadella viridis* L.) whose larvae and imagines inhabit wet meadows, and Chloropidea (Diptera) inhabiting exclusively herbaceous vegetation. The presence of Chironomidae and Culicidae and some remains of water-plants point to the existence of open fresh-water lakes, rivers, and lagoons. This is also indicated by the presence of Dolichopodidae whose larvae inhabit wet meadows, but whose imagines are predators feeding on small insects.

Such apparent contradictions depending on different environmental conditions of biocoenoses (either arid or humid) may be explained by differences in biotopes, conditioned by the meso-relief of the area and the existence of basins.

It must be noted that only one specimen of a cockroach was found, the optimal conditions for cockroaches being thickets in tropical forests with a high degree of humidity (Bey-Bienko 1950). On the basis of floral composition Palibin has defined

the average annual temperature of the area as greater than 20° C. Consequently temperature could not have been a limiting factor for the distribution of cockroaches; it must have been low humidity with sparse vegetation cover.

It should be pointed out that of all the psyllids described there is only one species of the subfamily Aphalarinae, *Agonosцена marmorea* B.-M., whose related Recent species, *Agonosцена targionii* Licht., lives on pistachio. Other representatives of this subfamily which are characteristic of the wormwood plant associations of desert and semi-desert are completely absent.

The above facts show that the climate of the Stavropol region in Karagan times was by no means of desert character but only slightly arid or moderately humid. The part of the Karagan basin described was considerably diluted with fresh water from the rivers. These conditions were favourable for life of some insects, such as the larvae of Trichoptera, water beetles (Dytiscidae and Hydrophilidae), Diptera-Culicidae and Chironomidae, and surface bugs (Gerridae), while land was characterized by a considerable variety of biocoenoses.

LITTORAL AND INLAND BIOCOENOSES OF STAVROPOL IN KARAGAN TIMES

On the basis of the palaeobotanical material, the study of the Homoptera, and the analysis of the composition of entomofauna and ecological data of present-day plants and insects, we may outline the following bioceoneses:

1. Biocoenoses of littoral and coast plant associations of the sea and brackish lagoons.
2. Biocoenoses of submerged and waterside plant associations of fresh-water basins.
3. Biocoenoses of flood-plain forests and tugai thickets.
4. Biocoenosis of deciduous-evergreen forest.
5. Biocoenosis of light, dry pine forest.
6. Biocoenoses of light, dry deciduous forests of savanna type and steppe shrub-growths.
7. Biocoenosis of coniferous forest.

BIOCOENOSES OF LITTORAL AND COAST PLANT ASSOCIATIONS OF THE SEA AND BRACKISH LAGOONS

From a description of the insect locality in the Stavropol region it may be concluded that the continental deposits of the Karagan layers in Vishnevaya Balka and Temnoleskaya were formed in the conditions of fresh-water lagoons with salinity no more than 5%. These conditions were favourable for the existence and development of water insects, as for instance, larvae of Trichoptera, may-flies (Ephemeroptera), dragon-flies (Odonata), surface bugs (Gerridae), water beetles (Dytiscidae, Hydrophilidae), larvae of Diptera-Chironomidae, and Culicidae. On the bottom of the parts of basins with quiet or sub-mobile water, as well as the larvae of benthic insects a great number of small *Spaniodontella* lived. These bivalves are found associated with *Unio*, *Planorbis*, and other fresh-water forms. They have no adaptation for burrowing and no siphons which are characteristic of the sub-littoral bivalve infauna.

The remains of marine plants are very rare. They have been found only in Temnoleskaya and Vlasova Balka and have been identified by Dr. I. V. Palibin as marine brown algae (*Cystoseira* sp.) and red algae (*Sphaerococcites* sp.).

The first inhabitants of the sandy coasts where the recession of the sea took place were herbaceous plants. Due to the tidal conditions of the sea-coast the majority of the species were probably halophytes which were unharmed by occasional submergence in sea-water and by the high salt content of the soil. The burial of herbaceous plants is very rare and there is but little chance of preservation of the imprints of plants so rare and few as the herbaceous pioneers of sandy shoals; the association corresponds to the *Pes-caprae* formation described by Richards (1952, p. 296).

Some of these plants penetrated inland, forming in places the biocoenosis of sandy dunes. Above the tidal zone and on steep slopes small and crooked trees and shrubs grew, scattered and in groups. In the formation of such biocoenoses the species of *Salix* played an important part, as well as grasses and other herbaceous monocotyledons which were the first to colonize the barren sandy coasts, shoals, and cliffs. These biotopes might have been occupied by *Myrica*?, *Elaeagnus*?, *Astragalus*?, various other trees and shrubs which could grow on poor soils, and also a herbaceous legume *Medicago* L.

Richer biocoenoses existed evidently on the banks of low-salinity lagoons and lemans and also river deltas. Some aquatic and riverside plants have been found in the Karagan layers of Stavropol: *Najadopsis dichotoma* Heer, *Phragmites oeningensis* A. Br., and *Dryopteris stiriaca* Ung. The present-day representatives of these genera also occur in the littoral associations of the sea and in river deltas (L. A. Sokolova *et al.* 1956, pp. 541–3). In the littoral zone reeds often form a 'sudd' (the term is used by Richards 1952) or floating sward on which *Dryopteris* and some other plants begin to settle. Besides the last named, *Carex* and *Nymphoides* most probably took part in the associations of deltas, and *Phragmites oeningensis* A. Br. grew on the margins of deltas and lemans. Further on along the river banks it was joined by *Dryopteris stiriaca* Ung., *Equisetum parlatorii* Schimp. and ?*Carex*. These were subsequently replaced by alder and willow over-growths and finally the latter gradually merged into the association of flood-plain humid forest.

BIOCOENOSES OF SUBMERGED AND WATERSIDE PLANT ASSOCIATIONS OF FRESH-WATER BASINS

Some fossil plants recorded from the Karagan layers of Stavropol enable us to assume the existence of several successive stages in the development of the vegetation of fresh-water basins, deltas, and low-salinity lagoons. This is also indicated by the composition of the entomofauna. The following three stages may be traced:

1. 'The association of the pond lily', the stage of bottom-rooted aquatic plants in which *Najadopsis dichotoma* Heer may be included. This biocoenosis of fresh-water basins (rivers and lakes) comprises also various groups of Karagan insects whose larvae or adults are associated with reservoirs; may-flies (Ephemeroptera), dragon-flies (Odonata), surface bugs (Gerridae), water-beetles (Dytiscidae, Hydrophilidae), caddis-flies (Trichoptera), and some Diptera-Culicidae, Chironomidae, and also predators Dolichopodidae.

2. 'The reed-swamp association.' This consists of a reed, *Phragmites oeningsensis*, and sometimes also the sedge (*Carex*). A leaf-hopper *Chloriona stavropolitana* B.-M. found in this biocoenosis is closely related to the present-day representatives of this species existing on *Phragmites communis* L. Although *Carex* has not so far been found among the Stavropol fossil plant remains, a leaf-hopper *Cicadella viridis* L. which has been recorded from Karagan strata can be seen on the recent species of *Carex*.

Richards (1952, p. 284) has noted that ferns occur in the 'Emergent aquatic associates'. In the river-side 'reed-swamp association' of the flood-plain in Middle Asia a fern *Dryopteris thelypteris* is found. It is possible that a fern *Dryopteris stiriaca* (Ung.) Palib. found in the Karagan layers and a horsetail *Equisetum parlatorii* Schimp. also formed part of this biocoenosis.

Again Richards (1952, pp. 293-4) noted: '... in the earlier phases of the hydrosere herbaceous plants are generally dominant; later they are replaced by woody plants. Both in temperate and tropical hydrosere monocotyledons play an important part in the intermediate stages. In temperate regions they dominate the reed swamp stage. ...' Many herbaceous plants, chiefly grasses (identified by I. V. Palibin under uncertain name *Culmis graminis*) formed part of this assemblage. The progress of this association stimulated the development of rich and varied groups of insects related to herbaceous plants. Thus the Tipulidae and Dolichopodidae whose larvae live either in water-logged soils or wet meadows were widespread with the development of the swamp meadow stacio.

3. 'Shrub association.' (This is the temperate zone analogue of the tropical 'Marsh shrub association'.) It consists of willow and alder thickets (*Salix lavateri* Heer and *Alnus kefersteinii* Goepf.). According to Richards's statement: '... in this process of *Verlandung*, or formation of new land from water, vegetation plays an essential part' (1952, p. 283). This association may be regarded as the last stage in the hydrosere and the beginning of the development of the forest association. It is the waterside character of this plant association that explains the wealth in species of willow psyllids.

As well as these plant associations of lakes and rivers on silty and clay soils, it is very probable that there were phytocoenoses on sand in whose formation the species of the genus *Salix* played an important part in addition to grasses and other herbaceous monocotyledons which were the first to colonize the sandy shores and cliffs. The variety of biocoenoses and the fact that the willow is not very particular about the soil is manifested by the number and variety in species of willow psyllids in the Karagan layers of Vishnevaya Balka.

Dalbergia bella Heer which occurred in the Stavropol flora of Karagan times might have been a relic of the previously mentioned 'Marsh scrub associates' (Richards 1952, p. 284) which in tropical conditions included some other species of the same genus. And yet we cannot place *Dalbergia bella* Heer in this particular phytocoenosis with certainty, as the species of this genus occur in the hylea and in dry *Shorea* forests. If *Dalbergia bella* Heer was a part in the 'Marsh scrub associates', it must have grown in the plant association *Salix-Alnus*, together with *Salix lavateri* Heer and *Alnus kefersteinii* Goepf.

Among the plants which may also be considered as belonging to the riverside biocoenosis it is possible to name the representatives of the family Myricaceae, two species of which occurred in Temnolesskaya (*Myrica olgae* Palib. and *M. salicina* Palib.) and one in Vishnevaya Balka. Probably there was also a representative of the *Elaeagnaceae* (*Elaeagnus*). In Recent times the representatives of the genus *Myrica* occur in the fringes of swamp forest, on seaside swamps, sandy shores, along streams, and on peaty bogs.

In the river-bank plant association *Terminalia miocaenica* Ung. might have been present as some species of this genus occur in riverside phytocoenoses, for instance in India. According to Richards this genus could have been a relic of the tropical riverside association. However, the presence of this plant does not give any reason to suppose that in Karagan times anything similar to a mangrove might have existed in the Stavropol region (Mchedlishvili 1951, pp. 921-3), because the species of the genus *Terminalia* grow above the tidal zone and are most frequently met with in biocoenoses of dry deciduous savanna and monsoon forests. There was no typical component of the 'Mangrove forest association' among the fossil plant remains.

BIOCOENOSSES OF FLOOD-PLAIN FOREST AND TUGAI THICKETS

As has been said the thickets of *Salix* and *Alnus* are the primary stage in the development of a forest association. On the low sides of rivers, lakes, and river-deltas in particular, the association of swamp forest might have developed as humid flood-plain forest and growths of shrubs on peaty soils. The floristic composition of such phytocoenoses most probably consisted of *Salix lavateri* Heer, *Alnus kefersteinii* Goepf., *Taxodium dubium* Sternb., and perhaps some species of the genera *Myrica* and *Ulmus*.

The group of willow psyllids is largely represented in the entomofauna of Vishnevaya Balka. Some Recent species live in light humid forests, on peat bogs, and on wet meadows along the watercourses. These are *Trioza striola*? Flor., *Psylla abdominalis*? M.-D., *Ps. pulchra*? (Zett.), *Ps. saliceti*? Forst., *Ps. moscovita*? Andr. Probably *Psylla adjuncta* B.-M. and *Ps. subambigua* B.-M. also inhabited similar biotopes.

The presence of psyllids inhabiting the humid stacio and peat bogs is good evidence that the light, humid deciduous forest on the flood plain might have existed.

In this biocoenosis, as well as willow psyllids, certain other forms might have lived: *Psylla ulmi*? Forst., a leaf-hopper of the genus *Eupteryx* (Cicadellidae), an arboreal mesophyte living on *Salix*, *Alnus*, etc.; a frog-hopper of the genus *Aphrophora* (Cercopidae), a habitant of trees and shrubs (*Salix*, *Alnus*), and herbaceous vegetation; also Tipulidea, soil gnats (Sciaridae), fungus gnats (Fungivoridae), scorpion flies (Mecoptera), etc.

On drier biotopes the river-bank vegetation changed considerably in the composition of forms and assumed most probably the character of the tugai thickets of the Middle Asian steppe areas. The composition of tugai associations apparently included willow and *Elaeagnus* thickets, and herbaceous plants such as grasses and legumes. The biocoenosis most probably consisted of willow psyllids (except those inhabiting peat-bogs) common to steppe and mountain regions: *Psylla klapaleki*? Sulc., *Ps. praevia*? Log., *Ps. moscovita* Andr., *Ps. propinqua*? Schaefer, *Ps. medicaginis*? Andr., *Trioza salicivora*? Reuter, *Tr. magnisetosa*? Log. The families Agromyzidae, Empididae, Syrphidae, and Sciaridae

appear with a richer development of herbaceous vegetation. This presumed phytocoenosis evidently alternated with meadow associations of grasses and legumes.

In the Karagan layers of Temnolesskaya the representatives of *Alnus*, *Taxodium*, *Equisetum*, and *Phragmites* have been found, also the remains of *Abies stavropolitana*, Palib. and some subtropical evergreens: Lauraceae, Myricaceae, Rosaceae (*Amigdalus*), Mimosaceae (*Acacia*), and various herbaceous plants. Evidently there was in the Temnolesskaya region a lowland area adjacent to the banks of a river-delta or perhaps a leman where a reed (*Phragmites oeningensis* A. Br.) grew near the shore and a horsetail (*Equisetum parlatorii* Schimp.) and a fern (*Dryopteris stiriaca* (Ung.) Palib.) were situated behind it, on the shore. Further inland alder thickets (*Alnus kefersteinii* Goepf.) appeared and there might have been a gradual transition from the latter to the association of a humid forest where *Taxodium dubium* Sternb. grew in the lower places and the oak (*Quercus aspera*?), *Viburnum*, *Ulmus* occupied a higher position. In the herbaceous ground flora *Dryopteris stiriaca* (Ung.) Palib. apparently alternated with grasses. The recorded frog-hopper of the genus *Aplrophora* lived on alder and willow trees and shrubs and on herbaceous plants.

This biocoenosis strongly resembles the *Colchis* alder and oak-alder lowland forests, though not so richly represented. The phytocoenosis evidently existed on clay and silty soils.

Other vegetative forms recorded from Temnolesskaya fossil plant remains by no means suggest that the continental biocoenoses were humid. These forms were *Amygdalus rodojovana* Ung., *Laurus lalages* Ung., *L. primigenia* Ung., and *Acacia parguriana* Ung. which were meso-xerophytic vegetative forms also taking part in other biocoenoses.

The entomofauna includes besides frog-hoppers of the genus *Aphrophora* a considerable number of butterflies (Lepidoptera, about 20%) and some bugs that may point to the existence in the Temnolesskaya region of open dry biocoenoses.

BIOCOENOSIS OF DECIDUOUS-EVERGREEN FOREST

The evergreens in the Karagan flora of Stavropol form a large proportion of the whole plant association. The present-day species of these genera are found mainly in the south subtropics of Asia and North America.

The floristic composition of the Stavropol deciduous-evergreen forest evidently comprised *Quercus aspera* A. Br., *Persea princeps* Heer, *Pinus saturni* Ung., *Sabal haeringiana* Heer, *Laurus primigenia* Ung., *L. lalages* Ung., *Cinnamomum scheuchzeri* Heer, *C. rossmasleri* Heer. Perhaps there were also *Terminalia miocaenica* Ung., *Dalbergia bella* Heer, and *Rhus obovata* Ett. Magnolias which are characteristic of humid biocoenoses are never met with in this phytocoenosis (*Flora of the USSR*, 1937, vol. 7). However, they occurred in the Karagan layers of Dagestan where they obviously formed part of more humid biocoenoses.

It is possible that in places the plant associations included also some of the Rosaceae: *Pyrus* in the shade; *Malus* and *Prunus* on exposed sites.

The biocoenosis obviously included a rich and varied fauna of insects. Among psyllids *Trioza cinnamomi*? Bos., *Tr. similis* B.-M., *Tr. interposita* B.-M., *Tr. subproximata* B.-M., *Agonoscena marmorea* B.-M., *Retracizzia andrianovae* B.-M., *Psylla loginovae* B.-M., *Ps. vasiljevi*? Suls, and *Ps. umbrata* B.-M. might have been in existence. Among

other groups of insects there might have been present a plant-hopper *Dictyophara* and some families of Diptera such as the Bibionidae, Agromyzidae, Sciaridae, Empididae, and Syrphidae.

BIOCOENOSIS OF LIGHT, DRY PINE FOREST

As has been said, in drier regions on sandy soils and slopes the oak forest was evidently replaced by the light, dry deciduous pine forest with a certain proportion of evergreen and deciduous subtropical flora such as palms, laurels (laurel, avocado), and herbaceous plants. This biocoenosis might have included also *Acacia parschlugiana* Ung. and possibly *Caragana* and *Pyrus*.

Among psyllids described there are no species whose host belongs to the genus *Pinus*. However, in a number of cases some closely allied species among the Recent representatives of psyllids (whose hosts are unknown) have been mowed down together with the herbaceous vegetation in the pine forest at the altitude of 2,000–3,000 m. For instance, a recent species *Trioza bifurcata* Tuth. is related to the fossil *Trioza interposita* B.-M. It should be noted that many adults of the recent species are met with on the pine in autumn though their hosts are other plants, e.g. *Psylla pulchra* (Zett.) feeding on the willow.

The psyllids feeding on leguminous shrubs (*Psylla longifurca* B.-M.) and on *Pyrus* (*P. vasiljevi*? Suls) as well as some frog-hoppers of the genus *Aphrophora* which are met with on conifers (*Pinus* and *Abies*) might have formed part of this biocoenosis.

BIOCOENOSSES OF LIGHT, DRY DECIDUOUS FOREST OF SAVANNA TYPE AND STEPPE SHRUB GROWTHS

The composition of the Karagan flora includes a certain proportion of drought-resistant and steppe-land forms that may point to the existence of dry steppe phyto-coenoses in Karagan times. Some of these plants evidently formed part in the composition of deciduous-evergreen forests on less humid biotopes preferring chiefly the margins or occupying exposed sunny mountain slopes covered with herbaceous vegetation, thus forming steppe-land shrub associations. These are *Amygdalus rodojovana* Ung., *Laurus primigenia* Ung., *L. lalages* Ung., and *Acacia parschlugiana* Ung.

Grassy legumes and leguminous shrubs such as *Caragana*, *Astragalus*, *Medicago* may also be added to this biocoenosis. Though their fossil remains are not known, the above-described psyllids live on them at present. *Pistacia*, on which may live *Agonocena marmorea* B.-M. may be included in this assemblage, as well as *Cotoneaster*, *Myrica*, and *Myrsine*.

The biocoenosis described may be subdivided into different associations depending on biotope and different soil types. It is possible to separate a group of plants growing on stony calciferous mountain slopes: *Amygdalus*, *Laurus*, *Prunus*, *Cotoneaster*, *Pistacia*, *Sorbus*, *Caragana*, *Astragalus*, *Medicago*. Some of them such as *Sorbus*, *Acacia*, *Caragana* occur on stony slopes on other substrata (*Flora of the USSR*, 1945, vol. 11). *Pistacia*, associated in places with *Amygdalus*, may belong to the driest biotopes (Korovin 1934, p. 372).

In the steppe zone the shrubs *Cotoneaster* and *Astragalus* grew in groups in the

association with grasses and herbaceous legumes (*Medicago*). On sandy mountain slopes and in dry regions the drought-resistant vegetation of *Astragalus*, *Valerianella*, and *Medicago* probably grew. In addition a number of species in both tree and bush form composed some kind of low mountain woodland of Middle Asia (Korovin 1934, p. 372). The biocoenosis included psyllids living on Rosaceae, Lauraceae, and Leguminosae, including *Psylla vasiljevi*? Sulč., *Ps. loginovae* B.-M., *Ps. stavropolitana* B.-M., *Ps. umbrata* B.-M., *Ps. elongata* B.-M., *Ps. cotoneasteris*? Log., and a group of leguminous psyllids including *Ps. longifurca* B.-M., *Ps. medicaginis*? Andr., *Ps. rhombifera*? Log., and also *Trioza uaguisetosa*? Log., *Agonoscena marmorea* B.-M., and *Retracizzia audriaenovae* B.-M. It is possible to include in this biocoenosis aphids, many of which live on *Acacia*, and *Chanithus vishueviensis* B.-M., a mesoxerophyll of steppe regions.

BIOCOENOSIS OF CONIFEROUS FOREST

Among the fossil remains of Vishnevaya Balka only three representatives of gymnospermous plants have been found: *Taxodium*, *Pinus*, and *Abies*. *Taxodium dubium* Sternb. apparently formed part in the biocoenosis of swamp forest and humid flood-plain forest; *Pinus saturni* Ung. in the biocoenosis of dry mixed forest. The latter was evidently the main representative in the association of dry pine forest with evergreen undergrowth on sandy soils, mountain slopes, and cliffs. As to *Abies stavropolitana* Palib., it could not have grown in the community with *Taxodium dubium* as the present-day representatives of the former are not tolerant of water-logged soils with a high water-table; but it could be included in the phytocoenosis with *Pinus saturnii* Ung., which can grow on mountain slopes with sufficiently fertile soils. This may be confirmed by the fact that *Abies stavropolitana* Palib. and *Psylla abietis* Kuw. feeding on it, were met with by chance (a single specimen of *A. stavropolitana* and two specimens of *Ps. abietis*); it is known that the further from the sea, a river mouth, or fresh-water basin the biocoenosis exists, the less is the possibility of burial of the flora and fauna. There are also species among the Karagan psyllids which at present inhabit the submontane, lower montane, and sub-alpine zones. This may indicate that such types of biocoenoses, and biotopes corresponding to them, may have been in existence in Karagan times.

Abies stavropolitana evidently grew in the submontane zone in pure stands or with the undergrowth consisting of willow (*Salix*) and mountain ash (*Sorbus*), both of which occur in the biocoenosis of pine and coniferous forests.

Among the herbaceous vegetation besides meadow grasses there were probably numerous ferns. In this biocoenosis *Psylla abietis*? Kuw. and *Ps. sorbi*? L. might have been present as well as some species of frog-hoppers of the genus *Aphrophora* and some aphids.

CONCLUSION

The method of actualism has often been successfully employed by scientists for the reconstruction of the earth's past and in their attempts to understand the organic and inorganic processes that took place in different periods of geological history.

This may be confirmed by lithological works of N.M. Strakhov (1960) and his followers. With no less success this method has been used by R. F. Hecker and his colleagues in

palaeoecological investigations at the Palaeontological Institute of the U.S.S.R. Academy of Sciences. However, these palaeoecological studies were generally concerned with the reconstruction of the environment of aquatic biocoenoses, particularly marine and more rarely those of fresh-water basins (Hecker 1948, 1965; Hecker, Osipova, and Belskaya 1963; Merklin 1950).

Fewer attempts have been made to reconstruct land biocoenoses. As a rule only the works of palaeobotanists and vertebrate specialists have been used, but of no less importance for the subject is the study in the palaeoentomology. The extensive biological relations of insects present abundant and valuable material for the indirect evidence that certain plants and animals existed though their fossil remains have not been found. The preliminary study presented in this paper is an attempt to reconstruct the phytocoenoses based not only on plant fossil evidence but also on the species of Homoptera.

Similar constant biological relationships which present plenty of material for the reconstruction of biocoenoses also exist in many other orders of insects (Hymenoptera, Diptera). For instance, phytophagous insects belonging to the subfamily Xyelinae (Hymenoptera) live only on the pine, each species of this family on a definite species of the genus *Pinus* (Rasnitsyn 1965). The same is observed among parasitic Hymenoptera: a list of hosts at whose expense one or another species of this group develops is often restricted to one or two species.

Among the representatives of Diptera there are also phytophagous insects, monophagous and oligophagous. These are various gall-flies (Cecidomyiidae), leaf-mining flies (Agromyzidae), Trypetidae, and other Diptera whose larvae live either on certain species or certain genera of plants. There are also predators and parasites belonging to this order, associated with certain species of the vertebrates or invertebrates. These include various gadflies (Oestridae, Hypodermatidae, Gastrophilidae), for instance a sheep botfly (*Oestrus ovis* L.) whose larvae parasitize the nasal chamber of sheep; the species of the genus *Rhinoestrus* whose larvae occur in the nasal chamber of the horse; and the species of the genus *Gastrophilus* which parasitize the intestines of the horse.

Various species of the families Dexiidae, Calliphoridae, Phasiidae, and Tachinidae are parasites on other insects, mainly monophagous or oligophagous. The larvae of the Dexiidae parasitize the larvae of Scarabaeidae; the larvae of the genus *Protocalliphora* and *Trypocalliphora* live in birds' nests and suck nestlings' blood; various Phasiidae parasitize bugs of the family Pentatomidae; the species of the genus *Pallenia* parasitize earthworms. The representatives of the families Syrphidae and Chamaemiidae partly belong to the active predators feeding on various aphids, coccids, and psyllids.

It is of particular interest to study aphids (Aphidea) for the reconstruction of phytocoenoses, as it enables us to establish double relationships of these insects with their primary and secondary host-plants. Palaeoentomological research in the Aphidea will also help to discover the cause and nature of rising migration and life-cycles in this interesting group of insects.

Thus for the reconstruction of organic and inorganic processes in the course of different periods of the geological history of the earth it is of great importance to adopt the method of actualism in the complex study of fauna and flora and their environment. When studying certain regions in this way, numerous facts of biological relationships of different groups of animals and plants with each other and with their environment,

will serve as a mutual corrective for the reconstruction of palaeobiocoenoses and their environments and will be the basis for the characteristic of climate and landscape of the past geological epochs.

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NEW VERTEBRATE EVIDENCE FOR A SOUTHERN TRANSATLANTIC CONNEXION DURING THE LOWER OR MIDDLE TRIASSIC

by J. F. BONAPARTE

ABSTRACT. Two species of therapsid reptile found in rocks of probable Lower Anisian age, in the Province of Mendoza, Argentina, are compared with similar forms from the Cynognathus Zone of South Africa. One of them is a dicynodont, *Kannemeyeria argentinensis*, which differs from the African form *Kannemeyeria erithrea* in only minor details. The other is a cynodont, *Pascualgnathus polanskii*, which shows very clear similarities to the African genera *Trirachodon* and *Diademodon*. The striking affinities of these Argentine species with African forms are interpreted by the author as evidence that Africa and South America were connected in some way during the Lower Triassic time.

THE concept of continental drift, first popularized by Wegener and du Toit, has been revived in recent years. However, it is now based upon a considerable variety of new types of observation. The analysis of submarine geology, palaeomagnetic data, geophysical measurements of heat flow in continental and oceanic regions, interpretation of earthquake zones, computer matching of continental shelf outlines, and other investigations, have all contributed to the revival of the idea that the present arrangement of the continents is the result of the break-up of an original supercontinent. These different geological investigations are in agreement with new palaeontological work on Triassic tetrapods from Argentina (Bonaparte 1966a), which seem to indicate that South America and Africa were directly connected with one another during the early Triassic.

Two therapsids have been collected in the central region of the Province of Mendoza, Argentina, south of the city of San Rafael, and were found in the upper part of the Puesto Viejo formation. This formation has been studied recently by Gonzalez Diaz (1964) and is exposed in a geomorphological district which he calls the Piedmont Elevation of Mendoza. One therapsid is a kannemeyeriid dicynodont, *Kannemeyeria argentinensis* Bonaparte (1966b); it is represented by a complete and well-preserved specimen. The other is a diademodontid cynodont, *Pascualgnathus polanskii* Bonaparte (1966b); this is also represented by excellent specimens.

Though this Puesto Viejo fauna is as yet known by these two species alone, it is clearly different from, and older than, the previously known Argentinian Triassic fauna of Ischigualasto (Romer 1962). The Puesto Viejo fauna instead appears to be contemporary with the cynodont *Colbertosaurus muralis* Minoprio (1954) from the Potrerillos formation of Mendoza. However, like other terrestrial faunas of the southern hemisphere, the Puesto Viejo fauna cannot be assigned to a precise period of the Triassic. As far as its age relative to the other faunas is concerned, it may be significant that the cynodont *Pascualgnathus* appears to be more advanced than the diademodontids of the Cynognathus Zone of South Africa in several features, i.e. in having a slightly longer secondary palate, larger canines, and sub-parallel tooth rows. If the Cynognathus Zone is provisionally regarded as Scythian in age, it would appear reasonable to regard the Puesto Viejo as of Lower Anisian age. This would imply that some elements of the

Scythian fauna survived into a later horizon in South America, just as they did into the later Ntawere and Manda formations of Africa (Attridge *et al.* 1964; Brink 1963).

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THE PUESTO VIEJO FAUNA

Kannemeyeria argentinensis

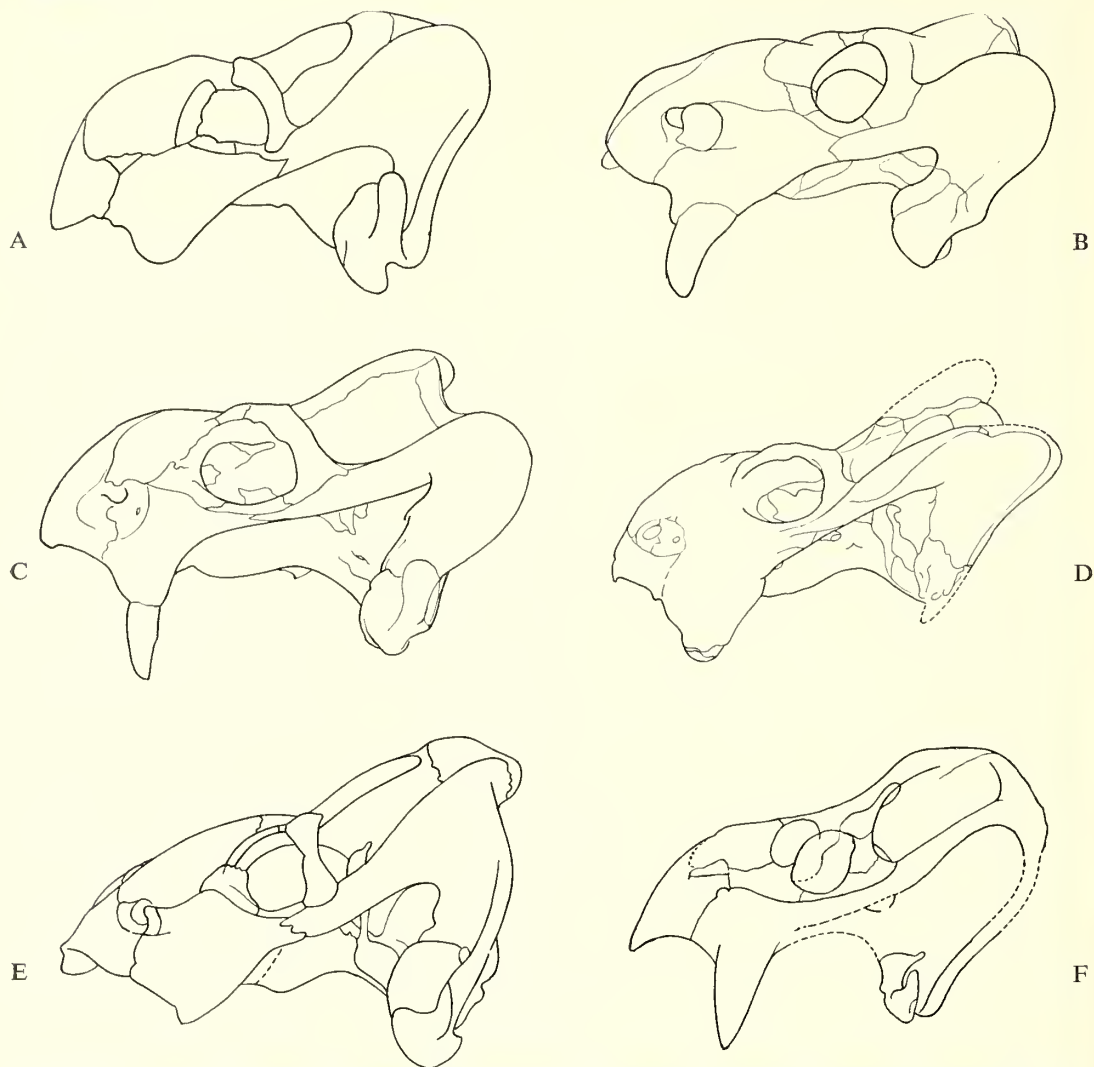
As can be seen from text-fig. 1, the new Puesto Viejo dicynodont is extremely similar to the South African genus *Kannemeyeria*, and is quite unlike the other known Triassic genera. In fact, no reason for separating it from the genus *Kannemeyeria* can be found, and its taxonomic status must therefore be established at the species level. The African species of *Kannemeyeria* are difficult to distinguish from one another; Cox (1966, pers. comm.) writes as follows: 'Unfortunately, as noted by Cruickshank (1965), the taxonomy of the South African species of *Kannemeyeria* is extremely obscure. However, the Argentinian form does appear to differ from *K. simocephalus* in lacking a fronto-nasal boss, and from *K. latifrons* in having ventrally (rather than antero-ventrally) directed canine tusks. In this last feature it is similar to the only other valid South African species, *K. erithrea*, and the skulls of these two forms are extremely similar. In the present state of our knowledge of the South African species, it is not possible to establish with certainty whether the Argentinian form is identical with *K. erithrea*, or whether it is specifically different.' The second, and somewhat more conservative course, of recognizing the Puesto Viejo form as a new species closely allied to *K. erithrea*, has provisionally been taken (Bonaparte, 1966a, 1966b). Some of the characters shared by *K. erithrea* and *K. argentinensis* are as follows:

1. The preorbital length is 30% and 31%, respectively, of the total length of the skull.
2. The structure of the 'narial depression', formed by maxilla, premaxilla, and septomaxilla.
3. The characters of the circumorbital bones, with similar rugosities on the prefrontal, frontal, and postorbital bones.
4. The characters of the 'lacrymal depression' that apparently communicates superficially with the 'narial depression'.
5. The exposure of the jugal in lateral view, behind the postorbital and above the squamosal.
6. The morphology of the maxilla and of its alveolar canine process.
7. The relation between jugal and maxilla below the orbit.
8. The characters of the median projection of the squamosal.
9. The pattern of ossification of the septosphenoid.
10. The topography of the parietal, and its relations with the squamosal.
11. The narrow parietal crest.
12. The projection of premaxilla posteriorly, separating the anterior ends of the nasals.

The differences between the two species are basically of a lesser degree, among which are a different extension of the epipterygoid ventrally, the presence of a ventral keel formed by both pterygoids, and the posterior projections of both squamosals, slightly more pronounced in *K. argentinensis*.

Affinities in the postcranial skeleton are evident between *K. argentinensis* and *Kannemeyeria* sp. illustrated by Pearson (1924), in the following aspects: the characters of the

pelvic girdle in the form of the ilium, the acetabulum and its borders, the proportions and the form of the ischia, and what can be seen of the pubis (incomplete in *K. argentinensis*).

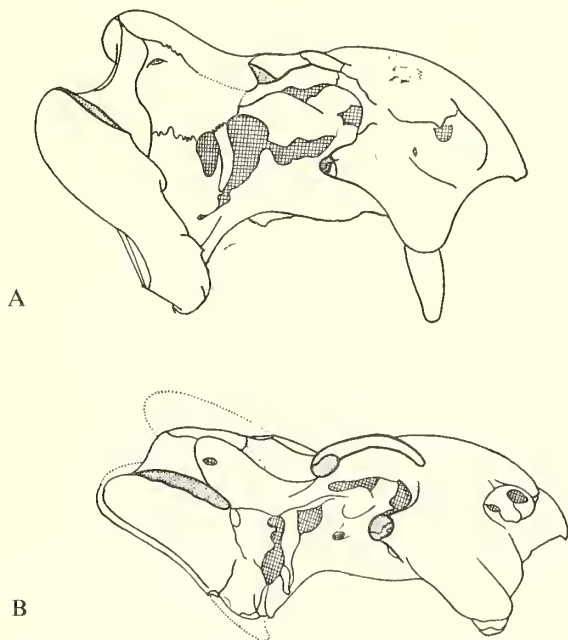


TEXT-FIG. 1. Skulls of some Triassic kannemeyeriids reduced to similar length, to compare with *Kannemeyeria argentinensis*. A, *Stahleckeria potens*, Brazil, after von Huene; B, *Dinodontosaurus turpior*, Brazil, after Cox; C, *Kannemeyeria argentinensis*, Argentina; D, *Kannemeyeria erithrea*, South Africa, after Watson; E, *Ischigualastia jenseni*, Argentina, after Cox; F, *Placerias gigas*, North America, after Cox.

Common characters of the hind limb are clear in the femur in nearly all its morphology, as for example in its flattened shape and in the relation between the femoral head and the trochanter major. The proportions of the femur differ in the two species; this may be due to their different size.

In the pectoral girdle there are affinities in the acromion process, the position of the coracoid foramen, and the depression which runs from this up the lower portion of the inner surface of the scapula.

In the humerus some affinities are noticeable and, bearing in mind the different size of the specimens compared, they are of interest. The well developed deltoid crest, the strong wide ectepicondyle, the well defined shaft in the middle of the humerus, are all characters common to both forms.



TEXT-FIG. 2. Lateral view of the skull, without the temporal and postorbital arches, of A, *Kannemeyeria argentinensis*, $\times \frac{1}{3}$; and B, *Kannemeyeria erithrea* (after Watson), $\times \frac{1}{7}$ approx.

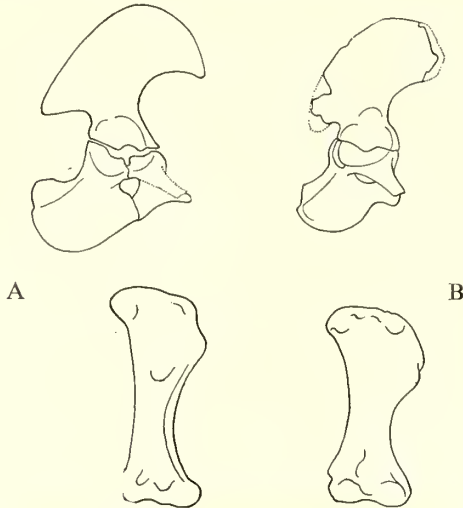
The ulnae of the two species are of different proportions: that of *K. argentinensis* is longer and thinner, but its proximal characters are very similar to those illustrated by Pearson. The few presacral vertebrae at our disposal and the few illustrated by Pearson show some common characters, such as the relative position of the zygapophysis and neural spine. The length of the vertebral centrum differs in the two species.

The skull of *K. argentinensis* is 26 cm. long, and that of South African species of *Kannemeyeria* ranges from 36 to 50 cm. long approximately. The difference of size is thus clear, and may well be the reason for the different proportions of some postcranial bones.

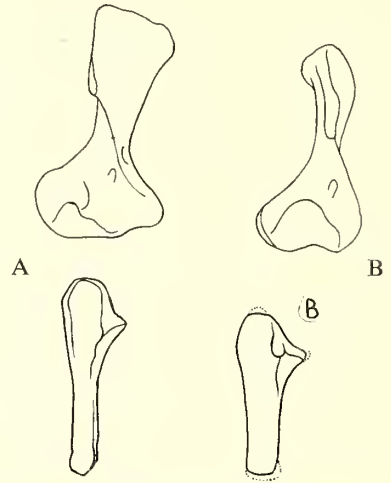
Pascualgnathus polanskii

This Puesto Viejo cynodont is of gomphodont type, but appears to be generically distinct from any previously known form. Though in some cranial characters it is

similar to *Exaeretodon*, the lumbar region is quite different. Furthermore, its dentition is different from that of *Exaeretodon*, *Ischnognathus*, and *Proexaeretodon* (which are all traversodontid cynodonts from the Ischigualasto formation of Argentina), and from that of *Traversodon* and *Gomphodontosuchus* (from the Santa María formation of Brazil). *Colbertosaurus muralis* from the Potrerillos formation of Mendoza (Minoprio 1954) appears to be a related form, but the only specimen known is an incomplete mandible with broken teeth. Finally, the cranial characters of *Pascualgnathus* differ from those of the Brazilian form *Belesodon*. Though it is thus quite unlike the South



TEXT-FIG. 3. Lateral view of the right pelvis, and ventral view of the right femur, of A, *Kannemeyeria argentinensis*, $\times \frac{1}{4}$; and B, *Kannemeyeria* sp. (after Pearson), $\times \frac{1}{2}$ approx.

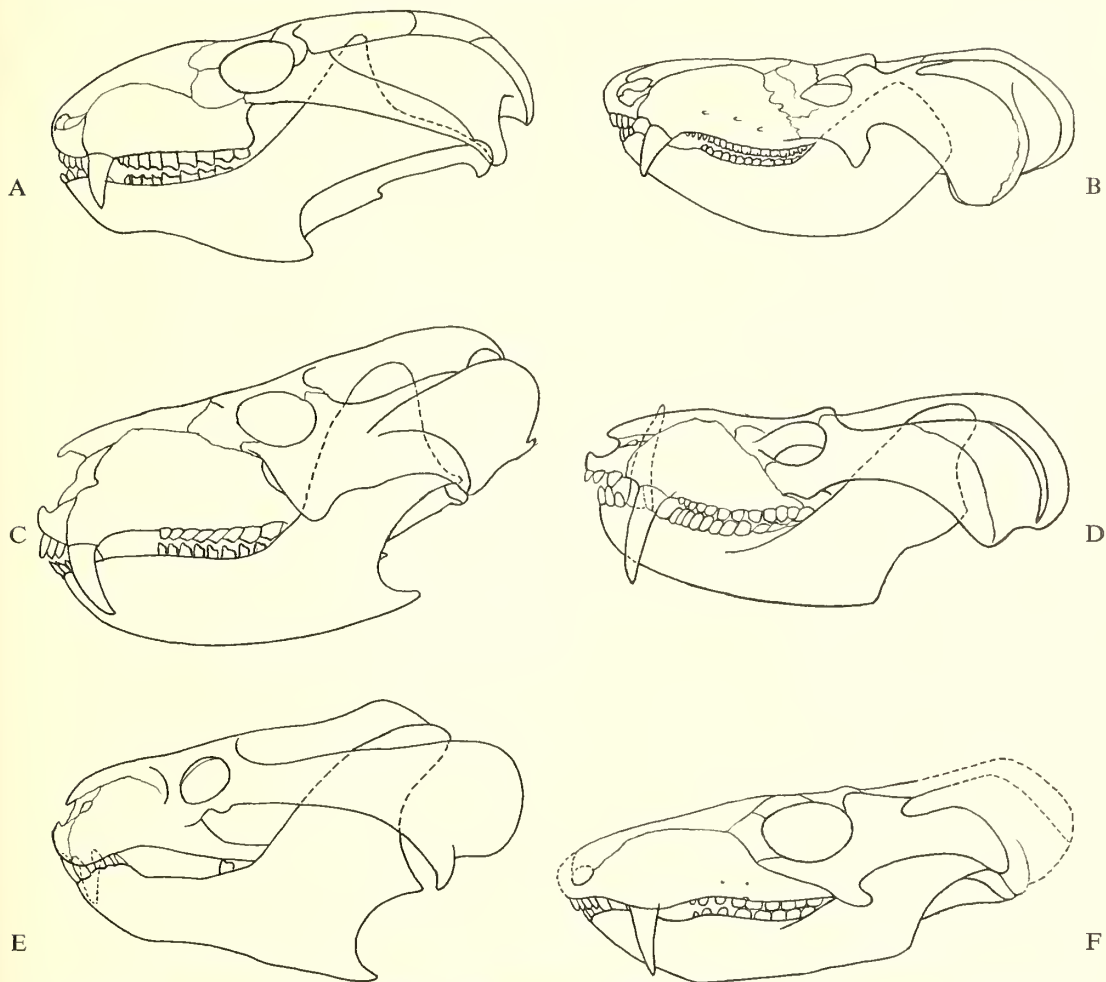


TEXT-FIG. 4. Ventral view of the humerus and median view of the ulna of A, *Kannemeyeria argentinensis*, $\times \frac{1}{4}$ and B, *Kannemeyeria* sp. (after Pearson), $\times \frac{1}{2}$ approx.

American genera, *Pascualgnathus* shows close similarities to the African genera *Trirachodon* and *Diademodon*, and it is thus considered as a diademodontid. The more obvious similarities between *Pascualgnathus* and *Trirachodon* are as follows:

1. The position of both postcanine rows is subparallel, with a minor outward divergence posteriorly.
2. Both have the same number of maxillary postcanine teeth.
3. More or less straight contact between each one of these teeth.
4. The first maxillary postcanines are small, and the others are progressively larger as far as the 7th–8th teeth, and then decrease posteriorly.
5. There are three teeth behind the level of the posterior border of the secondary palate.
6. There is a noticeable maxillary bulge from the row of teeth to the border of the maxilla.
7. There is a short diastema between the canine and the postcanine teeth (more pronounced in *T. berryi*).
8. The morphology of the choana roof (primary palate), up to the level where the pterygoids meet.
9. The position of the paracanine fossae.
10. The presence of a diastema between the incisor and canine teeth.
11. Both have the same number of incisor teeth, the third being the largest.
12. The characters of the area for the Jacobson's organ.
13. The apparent absence of the parietal foramen.

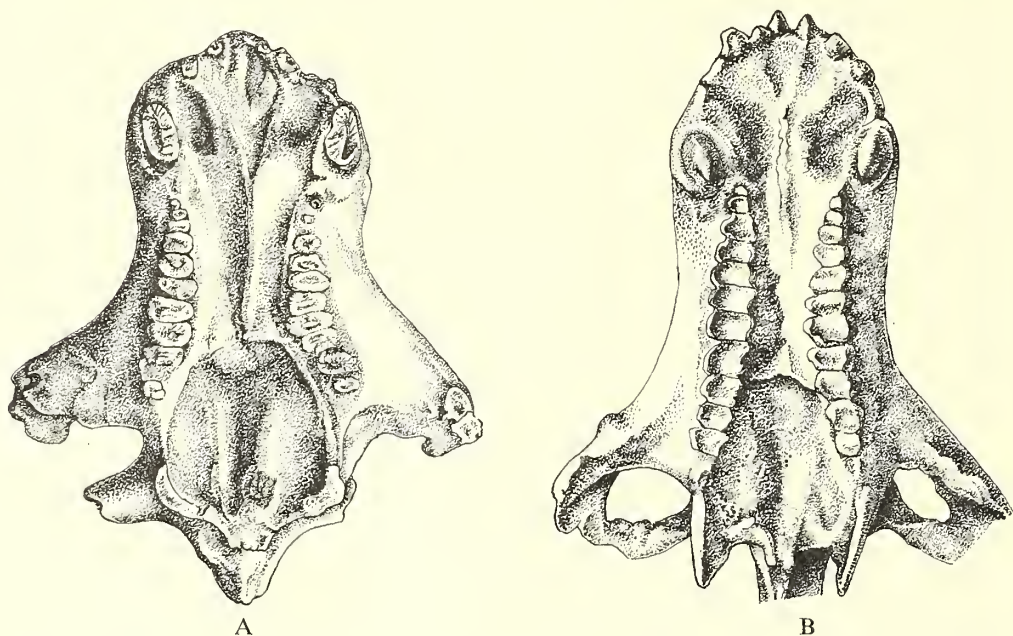
14. The parietal crest is thin and long.
15. There is an occipital crest which diverges slightly posteriorly.
16. The temporal fossae are lengthened and the temporal arch is subparallel to the axial plane.
17. The orbits are placed a little forward of the middle of the skull length.
18. The premaxilla extends anteriorly for a considerable distance beyond the canines.
19. There is a high coronoid process in the lower jaw.



TEXT-FIG. 5. Skulls and jaws of some Triassic gomphodont cynodonts, reduced to similar length, to compare with *Pascualgnathus polanskii*. A, *Traversodon stahleckeri*, Brazil, after von Huene; B, *Diademodon mastacus*, South Africa, after Brink; C, *Exaeretodon frenguelli*, Argentina, after Bonaparte; D, *Pascualgnathus polanskii*, Argentina; E, *Ischiognathus sudamericans*, Argentina, after Bonaparte; F, *Trirachodon kammeyeri*, South Africa, after Broom.

The principal affinities with *Diademodon*, besides some of general terms, are particularly striking in the braincase region: the topography of the parietal bone, the venous foramen between parietal, prootic, and alisphenoid, the characters of the 'foramen lacerum anterius', and the parasphenoid rostrum.

In the postcranial skeleton, many axial elements of good diagnostic value show great similarities between *Pascualgnathus* and *Diademodon*. A succession of 17 articulated vertebrae have been preserved in *Pascualgnathus*, including 9–10 presacral, 3–4 sacral, and 3–4 caudal, all with the ribs. The vertebral centra, as well as the ribs, are very much like those of '*Microgomphodon*' Seeley (1895), which is possibly a juvenile *Diademodon* (*vide* Brink 1955, p. 31); the relative size of the ribs, their relation to each other, and their form (especially of the sacral ribs) are very similar. Even though these axial elements



TEXT-FIG. 6. Palatal view of the skull of A, *Trirachodon berryi* (from Seeley), $\times 1$; B, *Pascualgnathus polanskii*, $\times 1$.

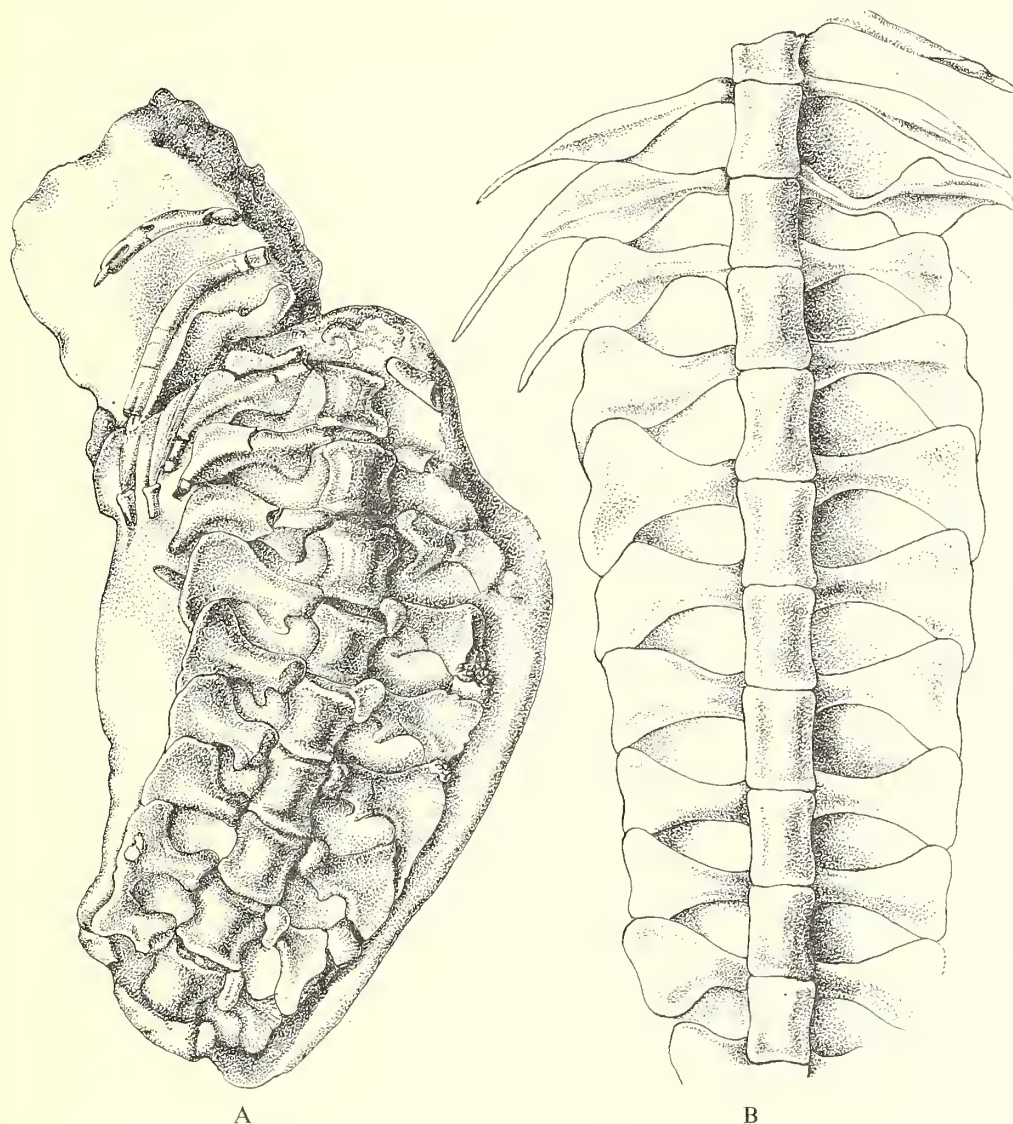
have been compared with those of a young specimen of *Diademodon*, the similarities observed seem highly significant.

It is possible to find resemblances in the other postcranial bones also. For the purposes of this paper the above points are adequate to establish that *Pascualgnathus polanskii* is a gomphodont cynodont related to the African diademodontids. Such characters as the hypertrophy of the canines, the absence of the internarial septum, the greater proportional extension of the secondary palate, and the smaller distance between the post-canine teeth rows, are anatomical features which suggest that *Pascualgnathus* may be more recent than the diademodontids from the Cynognathus Zone.

CONCLUSIONS

The significance of the similarity between these Argentinian species and the African forms must now be considered. Firstly, the characters of *K. argentinensis* appear to be more significant than those of *Pascualgnathus*. The kannemeyeriids, known from the

major part of Triassic times, are composed of a heterogeneous group of forms, and Cox (1965) has proposed their separation into three families. First Camp (1956) and later Cox (1965) have explained that adaptations to distinct herbivorous diets may be



TEXT-FIG. 7. Ventral view of presacral and two sacral vertebrae and ribs of A, '*Microgomphodon*' *oligocynus* (from Seeley), $\times 1$ (considered by Brink as a possible tiny *Diademodon*); B, *Pascualgnathus* *polanskii*. $\times 1$.

the cause of the noticeable strong variation in the skull morphology of these anomodonts. With this in mind, it is necessary to accept a great plasticity in the kannemeyeriids to react to different conditions, a fact which is in agreement with what is known of this

group. From this point of view, the affinities of *K. argentinensis* with the other species of the genus (especially *K. erithrea*) acquire great significance. Although the affinities of the cynodont *Pascualgnathus* with *Trirachodon* and *Diademodon* are somewhat less close, they are still of great interest. The cynodonts as a whole are apparently more conservative than the kannemeyeriids. Their evolutionary history is continuous, but is restricted to a single trend; as a result the South American, African, and the other cynodonts are comparable and their inter-relationships are more easily understood. However, this relative constancy and uniformity of the group within the cynodonts still seems inadequate to account for the extremely close affinity between *Pascualgnathus* and the African genera.

K. argentinensis and *P. polanskii* are thus very closely related to almost contemporaneous African forms. It is clear in the light of present knowledge that only a direct immigration from Africa to South America (or a common African-South American evolution), could explain such remarkable likeness between the therapsids from San Rafael, Argentina, and those from the Cynognathus Zone of Africa.

Among the works published in the symposium on *The Problem of land connection across the South Atlantic*, two papers on tetrapods (Romer 1952; Colbert 1952) discuss, from a different point of view, the probability of direct faunal interchanges between South America and Africa during Permo-Triassic times. Romer's conclusions were particularly liberal, recognizing the strong similarities between the Brazilian fauna (at that time the Ischigualasto and San Rafael faunas were unknown) and those of Africa, and accepting the direct interchange between the two southern continents as a possibility.

Among other authors that discuss the problem with analysis of Triassic tetrapods, Camp thought that, as far as the evidence from the Kannemeyeriidae was concerned, it seemed unnecessary to invoke theoretical southern connexions to explain the Triassic Dicynodont distribution: 'yet, the Dicynodont relationships do not entirely disprove such connections' (Camp 1956, p. 329). Reig (1962) accepted as a fact the immigration to South America of numerous Triassic tetrapods of 'Gondwana lineage', in our opinion without the necessary requirements of comparative analysis of the anatomy of the different groups involved.

Cox (1965) gives a list of the Triassic reptilian faunas of East Africa and South America, and considers different aspects of the relative ages of the faunas concerned. He suggests that the differences between the Argentine (i.e. Ischigualasto), Brazilian, and East African faunas could be explained either as resulting from their being of somewhat different ages or, alternatively, that the differences could be because they were on different continents. Cox mentions some conclusions on continental connexions by Creer (1964), but did not feel that there was sufficient evidence to permit a choice between these alternatives. We support, however, Cox's first alternative, that the Triassic fauna from Brazil and Argentina (only Ischigualasto), may be placed in the uppermost Middle Triassic or at least that of Ischigualasto more reasonably in the lowermost Upper Triassic and that, on the other hand, the East African Triassic faunas would be of Anisian age. The differences between these faunas are then due to their different ages.

As pointed out by Romer (1952, p. 250), to come to completely valid conclusions in relation to faunal connexions, the analysis must be based on comparisons of contemporary faunas. In this paper we have considered two species from Argentina of probable

Anisian age, with African genera of Scythian age. Nevertheless, the faunal elements known from Africa in recent years (Crompton 1955; von Huene 1942; Brink 1963; and others cited by Cox 1965) assigned to the lower Middle Triassic, show that such genera as *Kannemeyeria* and *Diademodon* survived beyond the Scythian Cynognathus Zone, into Anisian times. It does seem permissible, under these circumstances, to compare the Anisian San Rafael fauna with that of the Cynognathus Zone and, to some extent, with that of the Manda Beds.

The above affinities between the Argentine and African forms give good evidence of a type of direct faunal connexion which can only be interpreted as a solid continental union. The evidence for this conclusion meets the two fundamental requirements: (a) anatomical similarities of great significance, (b) very similar faunal ages.

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A MIDDLE TRIASSIC FLORA FROM THE CACHEUTA FORMATION, MINAS DE PETROLEO, ARGENTINA

by R. K. JAIN and T. DELEVORYAS

ABSTRACT. The fossil flora of the Triassic beds of Minas de Petroleo, a locality about 32 km. south-west of Mendoza in western Argentina (long. 69° 6' 25" W.; lat. 33° 3' 35" S.) is described. The strata belong to the Potrerillos Beds of the Cacheuta Formation of the Upper Gondwana of Argentina. The flora consists of about 34 species (3 new), belonging to about 20 genera (one new). Previously the flora of the Potrerillos Beds was known to consist of about 28 species. These beds were earlier referred to as the 'Rhaetic beds' and lately as of 'Lower to Middle Keuper' age, but the flora is now shown to be not younger than Middle Triassic in age.

THE fossils were collected from Minas de Petroleo in 1916-17 by the late Dr. G. R. Wieland, who never completed his study of the flora. The specimens, deposited in the Paleobotanical Collections of the Peabody Museum of Natural History at Yale University now bear official numbers referred to in the following pages. In addition to a couple of cards with collection data, there are also a few photographic negatives of some fossils, including those on which Wieland had published earlier (Wieland 1929), and two more on which he apparently had intended to report. Although the specimens in the unpublished photographs could not be located, they are being included in this paper.

STRATIGRAPHY

The Gondwanas of Argentina are divided into the Upper and Lower Gondwana. The Lower Gondwana or the 'Terreno de Paganzo' ranges from the earliest Carboniferous (perhaps with an Upper Devonian base) to the end of the Permian (Frenguelli 1950). Overlying the Patquia Formation of the Lower Gondwana are the so-called 'Rhaetic Beds' of the Upper Gondwana of Argentina (Krishnan 1954). These beds occur in the provinces of Mendoza, San Juan, La Rioja, and Patagonia, and are classified into various formations. The Cacheuta Formation of Mendoza represents one of the lowest formations in the Upper Gondwana of Argentina. Because of the existence of the so-called '*Thinnfeldia* flora' in these beds, they were earlier referred to as the 'Rhaetic beds' and later considered as 'Middle to Upper Keuper' (Groeber and Stipanovic 1952), and Middle Triassic to 'Infra-Liassic' (Frenguelli 1948). This subject is discussed further in a later part of this paper.

The Cacheuta Formation is further divided into four beds or 'Estratos':

4. Estratos de Rio Blanco
3. Estratos de Cacheuta { Upper
Lower
2. Estratos de Potrerillos
1. Estratos de la Cabras { 'Grupo del Cerro las Cabras' { Upper
Middle
Lower
'Fangalomerado' rojo

The rocks at Minas de Petroleo belong to the Potrerillos Beds (cf. Frenguelli 1944*b*, p. 557; 1948).

Minas de Petroleo is a well-known locality about 32 km. south-west of Mendoza in western Argentina (long. 69° 6' 25" W., lat. 33° 3' 35" S.). The outcrop is at the edge of an open region where the foothills rise rapidly. Wieland (1925) recognized seven zones in the 160-m. thick section rising from the Cacheuta volcanic base. Most of the plant fossils were found in laminated arenaceous to carbonaceous shales or fine clays in the second and third zones, starting from 10 m. above the volcanic base through a thickness of 70 m. Some ferns and Sphenopsida were found in a 10-m. thick zone (No. V) of shales and lesser conglomerates starting from 90 m. above the base.

Previous work. One paper by Wieland (1929) represents the only work on the plant fossils of the Triassic of Minas de Petroleo. He described some 'fruits' which he named *Fraxinopsis minor* and *F. major*, and a fragment of a leaf, which is now known as *Yabeiella wielandi* Oishi. However, much work has been done on other beds of the Cacheuta Formation. The main contributors to our knowledge of the flora of this formation were Geinitz (1876), Szajnocha (1889), Kurtz (1921), Wieland (1929), Oishi (1931), and Frenguelli (1941 *a, c*; 1942; 1943 *a, b*; 1944 *a, b, c, d*; 1946; 1947; 1948; 1950). As a result of their work about 20 species are known from Estratos de la Cabras, about 27 from Estratos de Potrerillos, and about 17 from Estratos de Cacheuta (Frenguelli 1948).

Materials and methods. Most of the fossils are only impressions; some are compressions having a thin film of carbon, but no cuticle. Only one specimen (1120) yielded some fragments of cuticles; these were removed with a scalpel and transferred to a watch glass, and treated for a few minutes with 'Clorox', a commercial bleaching solution containing 5.25% sodium hypochlorite by weight in an inert ingredient. In a few minutes the material was cleared; then it was thoroughly washed. A few fragments were stained with 2% aqueous safranin, and washed to remove the excess stain. The stained as well as the unstained fragments of cuticles were mounted directly in glycerine jelly.

SYSTEMATIC DESCRIPTIONS

Division BRYOPHYTA?, Class HEPATICA?, Order?, Family?

Genus *Thallites* Walton 1925

Thallites sp.

Plate 86, figs. 1-3

Material. Two specimens (1104 *a, b*) measuring 1-1.5 cm. in length, and *c.* 1 mm. in width above or below the dichotomy. In both the thalli branch twice dichotomously. A mid rib is recognizable in the middle of the thallus; no other structural details are discernible. Outline of thallus indistinct, uneven.

Remarks. Because there is no indication of natural affinities the specimens are referred to the form genus *Thallites* Walton (1925), defined to accommodate thalloid forms of uncertain affinities.

Division TRACHEOPHYTA

Subdivision SPHENOPSIDA

Order EQUISETALES

Family EQUISETACEAE

Genus *NEOCALAMITES* Halle 1908

Neocalamites carreri (Zeill.) Halle

Plate 86, figs. 4-6

Material. Four specimens (1095-7, 1106). 1095 (Pl. 86, fig. 4) is a stem fragment *c.* 12 cm. in length, and *c.* 3.5 cm. in width. It has two nodes separated by a 7-cm. long internode, one of the nodes being more distinct than the other. The surface shows 12-16 ridges per cm., alternating with furrows. It is not clear whether or not the ridges and furrows are continuous across the nodes.

At one of the nodes of the stem in 1096 (Pl. 86, fig. 5) there is a whorl of long linear leaves which are free to the base. The exact length of the leaves is not known, but they appear to be shorter than the internode, and measure *c.* 2 mm. in width. The internode in this specimen is *c.* 4 cm. long and has no visible surface markings.

1097 (Pl. 86, fig. 6) shows a detached nodal diaphragm *c.* 3 cm. in diameter. At its periphery is a whorl of leaves of which only the teeth-like basal parts are visible; faint further extensions indicate that the leaves were rather long as in 1096 (Pl. 86, fig. 5). An apparently similar diaphragm was described by Du Toit (1927) from the Molteno beds of the Karoo System of South Africa.

Genus *EQUISETITES* Sternberg 1933*Equisetites fertilis* Frenguelli

Plate 86, figs. 7-10

Synonymy. See Frenguelli 1944*c*, pp. 501-9, pl. 1-4.

Material. Four specimens (1104, 1107-9). 1107 (Pl. 86, fig. 7) is part of a stem, with small, basally united leaves covering a node. It measures *c.* 1 cm. in width at the level of the sheath. Leaves are free above with pointed acuminate apices. On either side are some long, leaf-like branches, like those seen in some of the living species of *Equisetum*, but no nodes are visible in them.

1108 (Pl. 86, fig. 8) shows a node with six pocket-like depressions, each of which has a tooth-like projection representing the base of a lost leaf. It is estimated that there were about twelve leaves at the node. No surface features are visible.

1109 (Pl. 86, fig. 9) shows a minute shoot apex and the last two visible nodes of the stem. It measures *c.* 0.8 cm. in length, *c.* 1.5 mm. in width at the node, and *c.* 1 mm. at the internode. It is difficult to ascertain the number of leaves enveloping the apex of the stem.

1104 (Pl. 86, fig. 10) is a detached nodal diaphragm *c.* 7 mm. in diameter. The margin is fimbriated as in the specimen illustrated by Frenguelli (1944*c*, pl. 5). No other details are discernible.

Subdivision PTEROPSIDA

Class PTEROPHYTA

Order FILICALES

Family OSMUNDACEAE

Genus *CLADOPHLEBIS* Brongniart 1849

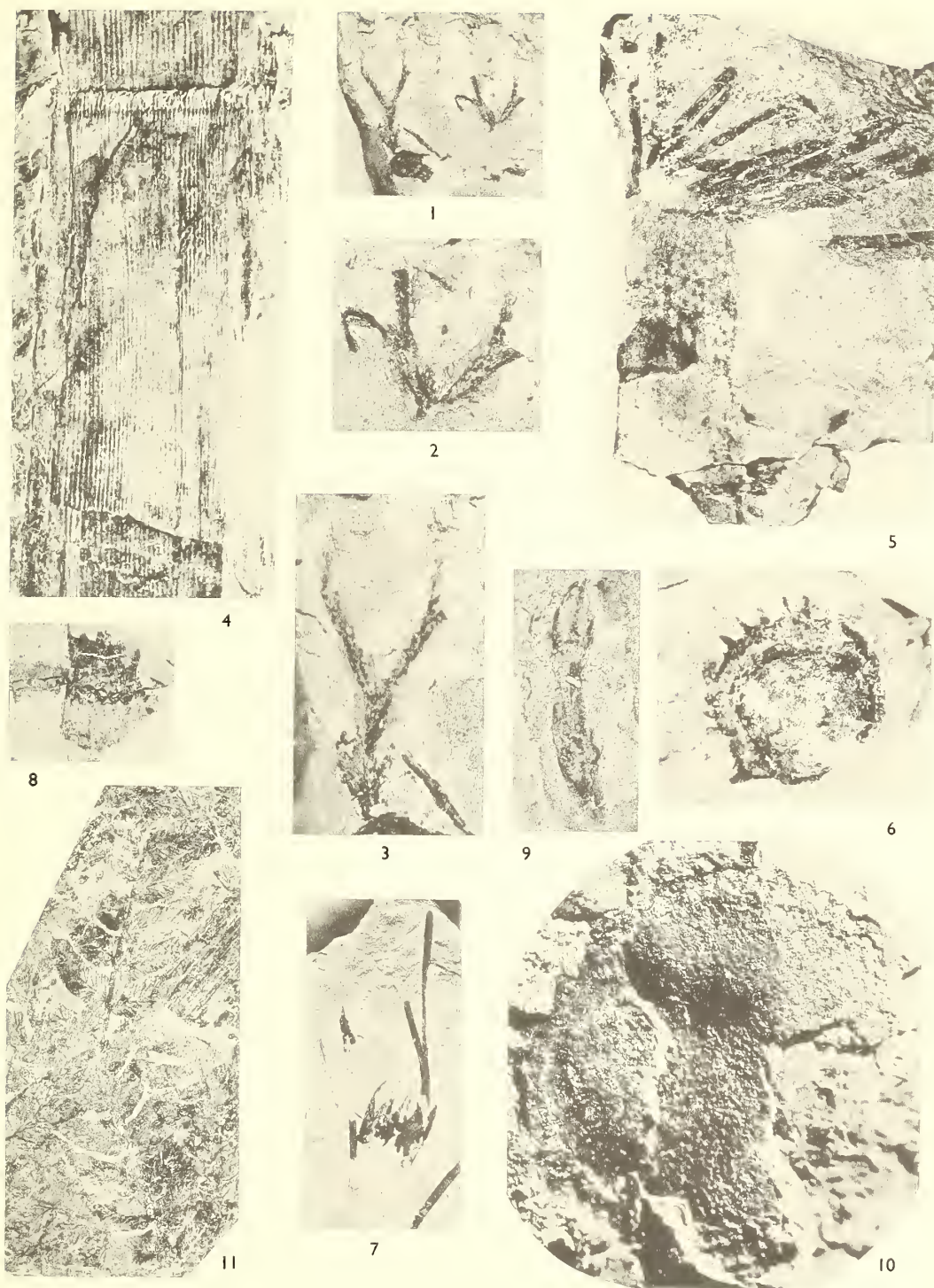
EXPLANATION OF PLATE 86

Figs. 1-3. *Thallites* sp. 1, 1104 *a, b*, $\times 1$; 2, 3, the same, $\times 2.5$.

Figs. 4-6. *Neocalamites carreri* (Zeill.) Halle. 4, 1095, indicating a node, and longitudinal ridges and furrows on the stem, $\times 1$; 5, 1096, stem with a whorl of leaves at a node, $\times 1$; 6, 1097, a nodal diaphragm, $\times 1$.

Figs. 7-10. *Equisetites fertilis* Frenguelli. 7, 1107, a node with a whorl of leaves, $\times 1$; 8, 1108, a node showing bases of leaves, $\times 1$; 9, 1109, stem apex covered with young leaves, $\times 5$; 10, 1104, a nodal diaphragm, $\times 10$.

Fig. 11. *Cladophlebis kurtzi* Frenguelli. 1106, a pinna, $\times 1$.



Cladophlebis kurtzi Frenguelli

Plate 86, fig. 11; Plate 87, figs. 1, 2

- 1921 *Asplenium whitbyense* Heer; Kurtz, pl. 16, figs. 202 *a, b*.
1927 *Cladophlebis uebensis* (Brongniart) Nath.; Du Toit, p. 321, fig. 2.
1947 *Cladophlebis kurtzi* Frenguelli, pp. 52–53, pl. 4, figs. 4–6; pl. 6, fig. 2 (?).

Material. Three specimens (1059, 1060, 1116), consisting of a large number of frond fragments lying close to, and overlapping each other. The pinna rachis is conspicuous, with pinnules attached closely by broad bases. Pinnules are small, *c.* 1 cm. long and 5–6 mm. broad at the base, oblong with an entire margin and obtusely rounded apex. Sometimes pinnules are slightly curved distally. Each pinnule has a distinct mid rib, and fairly steep and close lateral veins. Each lateral vein forks once close to the mid rib, and again at half the distance between the mid rib and the margin of the pinnule. Near the margin, all the branches of the lateral veins are almost equidistant from each other.

Remarks. This species was earlier identified as *Asplenium C. whitbyense* (Kurtz 1921), and later as *C. nebensis* (Du Toit 1927), but it differs from both in essential details. In *C. nebensis* (Brongn.) Nath. the lateral veins are forked only once (Brongniart 1828, pl. 98, fig. 3), whereas in *C. kurtzi* the lateral veins normally fork twice.

Cladophlebis mesozoica Kurtz

Plate 87, figs. 3–6

- 1947 *Cladophlebis mesozoica* Kurtz; Frenguelli, pp. 59–60, pl. 6, fig. 5; pl. 7B.
1947 *Cladophlebis concinna* (Presl) Du Toit; Jones and de Jersey, p. 12, text-fig. 4 (pl. 1, fig. 4).

Material. Three specimens (1059, 1060, 1118). 1059 (Pl. 87, fig. 3) is a part of a bipinnate frond with a rachis *c.* 3 mm. thick, and bears two rows of opposite pinnae, each generally more than 7.5 cm. long. 1060 (Pl. 87, figs. 4, 5) shows a slender pinna rachis bearing distantly and alternately arranged pinnules. Each pinnule is attached by its broad base, measures *c.* 1.5 cm. in length, 8–9 mm. in width at the base, and has a more or less entire margin, and short acute apex. Further, each pinnule has a distinct mid rib with twice-forking, alternate lateral veins, the ultimate branches of the latter tending to become parallel toward the margin.

Remarks. There is a superficial resemblance between this species and *C. kurtzi*, but a closer study indicates that *C. mesozoica* differs in having distantly and alternately arranged pinnules with acute apices, as opposed to the closely and oppositely arranged pinnules with obtuse apices in *C. kurtzi*.

Similar specimens illustrated by Jones and de Jersey (1947) were erroneously compared with *Cladophlebis concinna* (Presl) Du Toit (1927, p. 318, pl. 17, fig. 1). The latter species differs from *C. mesozoica* in having almost overlapping leaflets with rounded apices, and typically once-forked lateral veins.

Cladophlebis johnstoni Walkom

Plate 87, figs. 7, 8

- 1925a *Cladophlebis johnstoni* Walkom, p. 76, figs. 2, 2a.

- 1947 *Cladophlebis mendozaensis* Geinitz; Frenguelli, pp. 60-63, pl. 8B; pl. 9, figs. 2, 3 (others?); pl. 10, figs. 1-3, 8 (others?); pl. 11; pl. 12, figs. (1-3?).

Material. Two specimens (1057, 1111). 1111 (Pl. 87, figs. 7, 8) shows the terminal part of a frond with pinnae varying in length from less than 0.5 cm. at the apex, to 2.3 cm. at the base, and with entire to broadly crenate margins. Lateral veins fork one to three times. Each lobe of a pinna has an independent set of veins, indicating the equivalence of a lobe to a pinnule.

Remarks. Frenguelli (1947) had referred many specimens of this species to *C. mendozaensis*, a species based primarily on a very fragmentary specimen described and poorly illustrated by Geinitz (1876, pl. 2, fig. 4). The latter differs from *C. johnstoni* in most of the structural details of the pinnule, such as shape, margin, and venation.

Cladophlebis australis (Morris) Seward

Plate 88, figs. 1-4; Plate 89, fig. 11

Synonymy. See Frenguelli 1947, pp. 56, 57, pl. 2, figs. 8-10.

Material. Four specimens (1053, 1055, 1056, ?1117), showing a typical bipinnate frond with a stout rachis measuring up to 6 mm. in width. Pinnae are alternate, forming angles of about 50° with the rachis. Pinnules are alternate to sub-opposite, lanceolate, and attached to the pinna rachis by the whole base. Each pinnule has a broad base, entire or slightly undulate margin, shortly acute or sometimes more or less truncate apex, up to 2.5 cm. in length, and 0.6 cm. in width at the base. The mid rib of each pinnule tends to fade out towards the apex. Lateral veins arise at acute angles from the mid rib and typically fork twice, the ultimate branches tending to become parallel near the margin. In 1053 (Pl. 89, fig. 1) the shape and attachment of the pinnules appear a little different from those of the other specimens; however, venation appears to be essentially of the same type; it is only tentatively referred to this species.

EXPLANATION OF PLATE 87

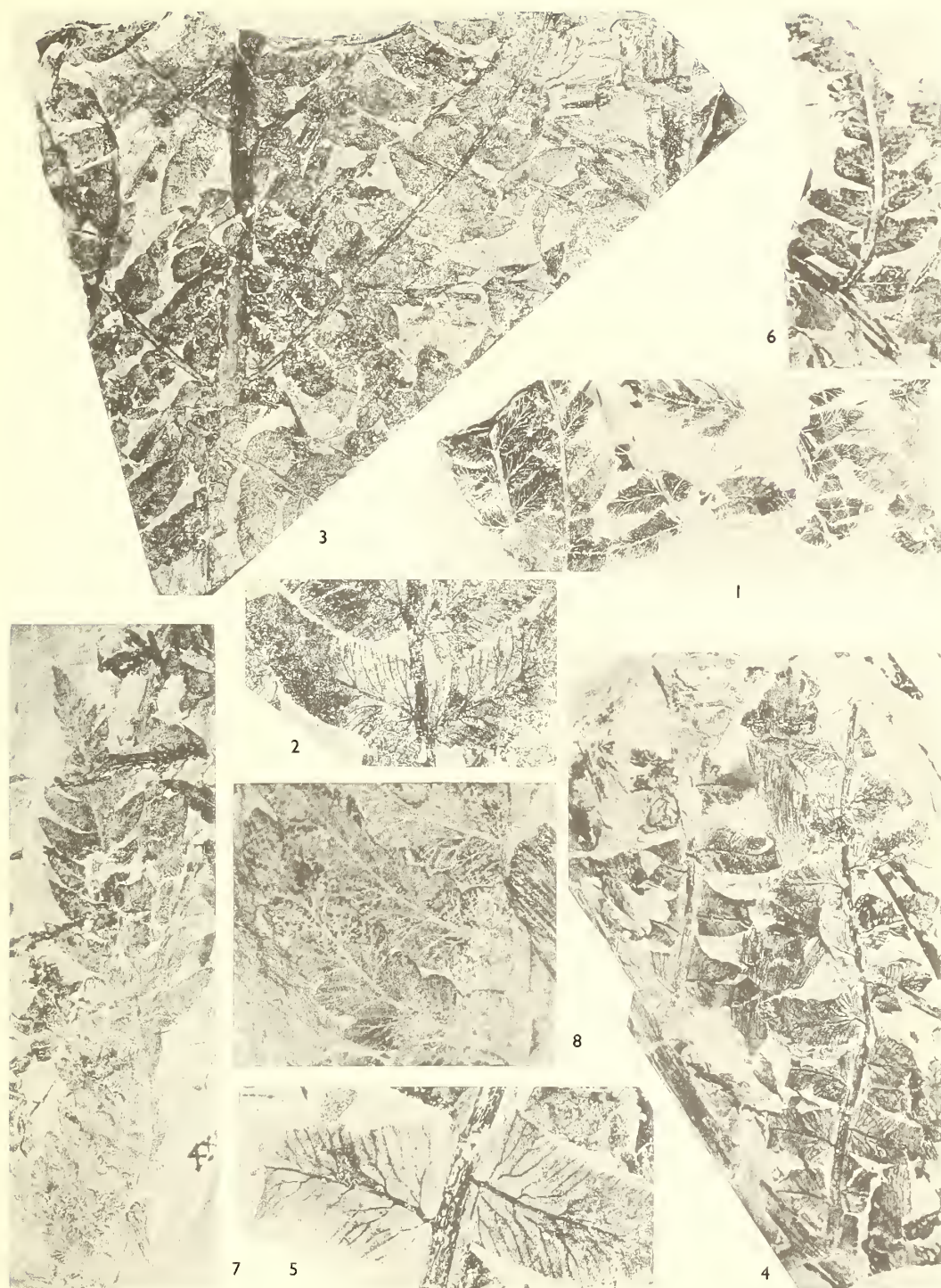
- Figs. 1, 2. *Cladophlebis kurtzi* Frenguelli. 1, 1115, fragments with closely set pinnules, $\times 1$; 2, part of 1116 showing veins, $\times 2.5$.
 Figs. 3-6. *Cladophlebis mesozoica* Kurtz. 3, 1059, indicating part of a bipinnate frond, $\times 1$; 4, 1060, showing shape and attachment of pinnules, $\times 1$; 5, part of above showing venation, $\times 2.5$; 6, 1118, a small pinna, $\times 1$.
 Figs. 7, 8. *Cladophlebis johnstoni* Walkom. 7, 1111, part of a frond, $\times 1$; 8, part of above showing veins, $\times 2.5$.

EXPLANATION OF PLATE 88

- Figs. 1-4. *Cladophlebis australis* (Morris) Seward. 1, 1055, part of a bipinnate frond, $\times 1$; 2, part of above showing veins, $\times 2.5$; 3, 1117 indicating shape of pinnules, $\times 1$; 4, 1056, apical part of a pinna, $\times 1$; 4, 1056, apical part of a pinna, $\times 1$.
 Figs. 5, 6. *Cladophlebis* sp. 5, 1112, $\times 1$; 6, 1113, $\times 1$.

EXPLANATION OF PLATE 89

- Fig. 1. *Cladophlebis* sp. 1053, $\times 1$.
 Figs. 2, 3. *Cladophlebis wielandi* sp. nov. 2, 1054, parts of two pinnae, $\times 1$; 3, part of above showing venation, $\times 2.5$.
 Figs. 4, 5. *Sagenopteris longicaulis* Du Toit. 4, 1137a, a more or less complete leaflet, $\times 1$; 5, parts of leaflets with details, $\times 2.5$.
 Fig. 6. *Dicroidium odontopteroides* (Morris) Gothan. 1051, distal part of a forked frond, $\times 0.5$.



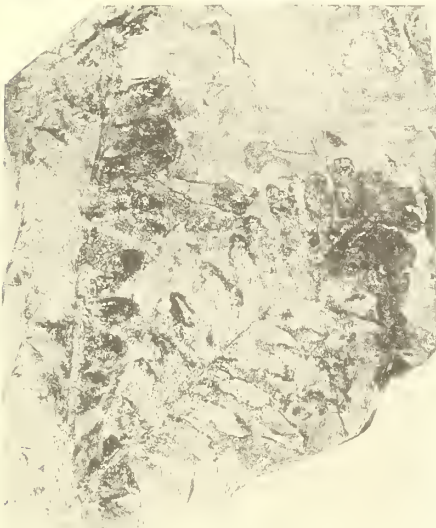




3



2



6



1



5



4

Cladophlebis wielandi sp. nov.

Plate 89, figs. 2, 3

1947 *Cladophlebis concinna* (Presl) Du Toit; Jones and de Jersey, p. 12, text-fig. 5, pl. 1, fig. 4?*Holotype*. 1054 (Pl. 89, figs. 2, 3).

Material. Holotype only, showing two pinnae of a frond, probably still connected with the rachis (but not exposed by preparation because of other overlying significant specimens). Preservation good, with excellent details of pinnule venation.

Diagnosis. Leaf bipinnate, pinnules alternate to sub-opposite, fairly closely spaced, attached to the pinna rachis at angles of about 70°, *c.* 1.5 cm. in length, oblong-lanceolate with serrate margin, and acute apex; mid vein of each pinnule forked at the apex; lateral veins few, typically forked only once, rarely with a second dichotomy in one of the branches of the lateral veins.

Remarks. This species is closely associated with *Cladophlebis mesozoica* Kurtz, but it differs from the latter in having closely spaced pinnules with serrate margins, and a once-forking system of lateral veins, as opposed to the widely spaced alternate pinnules with almost entire margins and typically twice-forked lateral veins in *C. mesozoica* Kurtz.

The new species, however, shows some resemblance to *C. denticulata* (Brongn.) Fontaine, and *C. sewardi* Johansson. It is similar to *C. denticulata* in having pinnules with serrate margins and once-forking lateral veins, but differs in having shorter pinnules, a less acute apex, and fewer veins.

There is a greater resemblance between this species and *C. sewardi* (Johansson 1922, pl. 1, fig. 42), but it differs from the latter in lacking the regular second dichotomy of the lateral veins.

Cladophlebis sp. indet.

Specimen 1112 (Pl. 88, fig. 5) shows either the subterminal portion of a frond or part of a pinna of a large bipinnate frond. The rachis is *c.* 1 mm. in width, and has opposite to sub-opposite pinnules arranged in two rows. Pinnules are somewhat curved distally, up to 2 cm. in length and 7 mm. in width at the base. Each pinnule is lanceolate with a crenate margin and acute apex. Veins are poorly preserved.

This specimen appears similar to one of Frenguelli's specimens (Frenguelli 1947, pl. 9, fig. 5) referred to *Cladophlebis mendozaensis*, but it is hard to justify its identification with that species. It may be an ill-preserved specimen of *C. johnstoni*.

Specimen 1113 (Pl. 88, fig. 6) is similar to 1112, but the pinnules appear to be more slender in form and attached at wider angles. It may be related to one of the species described above, but superficially it resembles *C. integra* (Oishi and Tanah) Frenguelli (Frenguelli 1947, p. 35, fig. 21), and *C. indica* (Oldh. and Morris) Feistmantel (Oldham and Morris 1862, pl. 27, fig. 2).

Class CAYTONIALES

Genus SAGENOPTERIS Presl 1838

Sagenopteris longicaulis Du Toit 1927

Plate 89, figs. 4, 5

Material. Overlapping fragments of one or more specimens collectively numbered as 1137*a-d*. Because of crowding, precise outline of individual leaflets is not clear. Each leaflet is *c.* 6 cm. in length, and has

a distinct mid rib and many lateral veins, the latter forming angles of about 65° with the mid rib. Lateral veins are a little less than 1 mm. apart and start branching and anastomosing freely only a short distance from the mid rib.

Class CYCADOPHYTA
Order PTERIDOSPERMALES

Family?

Genus THINNFELDIA Ettingshausen 1852

Thinnfeldia dutoiti sp. nov.

Plate 90, fig. 4

1927 *Thinnfeldia rhomboidalis* Ettings.; Du Toit, p. 340, text-fig. 6c.

Holotype. 1046 (Pl. 90, fig. 4).

Material. Holotype only, measuring c. 8 cm. in length.

Diagnosis. Leaves pinnate (as far as known); rachis slender; pinnules widely spaced, alternate to sub-opposite, attached by their whole bases, rhombic with more or less acute apices; four or more veins entering each pinnule, each vein forking once or twice.

Remarks. *Thinnfeldia dutoiti* differs from *T. rhomboidalis* Ettings. in having less slender leaflets, lacking a thickened margin and distinct mid rib. Townrow (1957) has also indicated that these species are different from each other.

Townrow (1957) is openly suspicious about the existence of *Thinnfeldia* in the Mesozoic floras of the Southern Hemisphere. All the specimens hitherto known from Gondwanaland, and earlier referred to this genus, probably belong to *Dicroidium* Gothan. But in the absence of any indication of dichotomy of the fronds, this species is referred to *Thinnfeldia*.

Thinnfeldia praecordillarae Frenguelli (1944c)

Plate 90, figs. 7, 8

Material. Two specimens (1044, 1052). 1052 is c. 8 cm. in length. It has a distinct rachis bearing two rows of pinnules; the pinnules are alternate, small, up to 5 mm. in length, and elliptical in shape. Each pinnule has a small mid rib, which gives off a number of small simple (all?) radiating veins. 1044 (Pl. 90, fig. 8) has more or less semicircular pinnules.

EXPLANATION OF PLATE 90

Figs. 1-3. *Dicroidium odontopteroides* (Morris) Gothan. 1, 1048, showing veins in some pinnules, $\times 1$; 2, 1047, showing lanceolate pinnules with characteristic venation, $\times 1$; 3, 1088, basal part of a forked frond, $\times 1$.

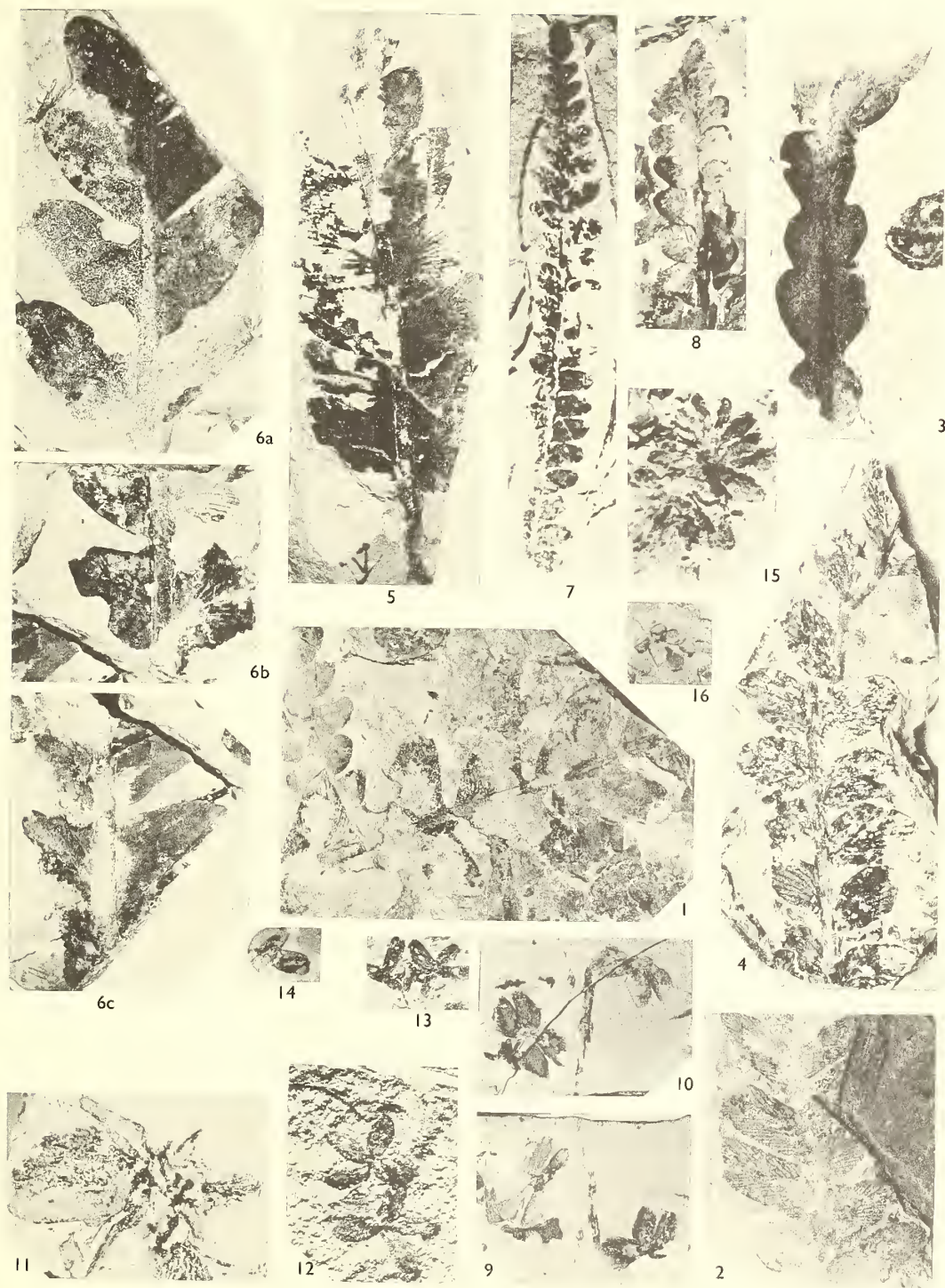
Fig. 4. *Thinnfeldia dutoiti* sp. nov. 1046, $\times 1$.

Figs. 5, 6. *Dicroidium feistmanteli* (Johnston) Gothan. 5, 1045, with veins in parts of some pinnules $\times 1$. 6a, 1050; 6b, 1119; 6c, 1049; three fragments of fronds, $\times 1$.

Figs. 7, 8. *Thinnfeldia praecordillarae* Frenguelli. 7, 1052, showing smaller and oblong pinnules, $\times 1$; 8, 1044, with larger and semicircular pinnules with distinct mid ribs, $\times 1$.

Figs. 9, 10, 14-16. *Incertae sedis*. 9, 1128, $\times 1$; 10, 1129, $\times 1$; 14, 1130, $\times 1$; 15, 1136, $\times 3$; 16, 1101, $\times 1$.

Figs. 11-13. *Fanerotheca extans* Frenguelli. 11, 1099, $\times 4$; 12, 13, printed from Wieland's photographic negatives, magnification unknown.



Remarks. Some specimens figured by Walkom (1928, pl. 26, figs. 1, 2) from the Esk district of Queensland were described by him as fertile specimens of *Todites williamsoni*. However, neither in the description nor in the illustrations is there any convincing evidence of this. If that is the case, they do not appear to be different from the present material of this species.

Family CORYSTOSPERMACEAE
Genus DICROIDIUM Gothan 1912

Dicroidium odontopteroides (Morris) Gothan

Plate 89, fig. 6; Plate 90, figs. 1–3

Synonymy. See Townrow 1957, pp. 33–39.

Material. Four poorly preserved specimens (1047–8, 1051, 1088). 1051 (Pl. 89, fig. 6) shows distal part of a forked frond, each half up to 13 cm. in length with an axis *c.* 2 mm. wide. Pinnules are sub-opposite, smaller in size near the base and apex, and larger between. The largest pinnule is *c.* 2.5 cm. in length, and 0.5 cm. in width at the base. Each pinnule is attached to the rachis by its whole broad base, and has an entire margin, and shortly acute apex. The veins are not visible. Venation, visible in 1048 (Pl. 90, fig. 1) and 1047 (Pl. 90, fig. 2) is typically without a mid rib. In 1047 the pinnules are lanceolate. In 1088 (Pl. 90, fig. 3) the pinnules appear as lobes of an undivided lamina.

Remarks. All the specimens described are either small fragments or are very badly preserved. However, together they justify their inclusion in this species. But for the merger of *Dicroidium lancifolium* in *D. odontopteroides* (Townrow 1957), some of the specimens could certainly be identified with *D. lancifolium*.

Dicroidium feistmanteli (Johnston) Gothan

Plate 90, figs. 5, 6

Synonymy. See Townrow 1957, p. 39.

Material. Four specimens (1045, 1049–50, 1119) showing fragments of fronds with closely arranged sub-opposite pinnules on a rachis. The pinnules are rather expanded, broader distally than at the base. There is no mid rib, and all the veins tend to converge toward the base, but they do not meet at the same point.

Remarks. The specimens could almost as well be referred to *Dicroidium* (*Zuberia*) *zuberi* (Szajnocha) Townrow (1957). Although it is difficult to distinguish between the leaves of these two species, Townrow (1957) declined to express any opinion about this species, presumably because of its reported association with peculiar fructifications that are never found associated with *D. feistmanteli*. Because no such fructifications occur in association with the leaves described above, it is reasonably safe to refer these specimens to *D. feistmanteli*.

Also, without cuticles it is difficult to distinguish between *Dicroidium* and *Hoegnia* (Townrow 1957), and none occurs.

Dicroidium coriacium (Johnston) Townrow

Plate 91, figs. 1, 2

Synonymy. See Townrow 1957, p. 45.

Material. Five poorly preserved specimens (1908–93), up to 10 cm. in length, and forking once at some distance (about one-third of the length of the leaf) above the base. The margin varies from entire to broadly crenate, even in the same leaf. Each marginal projection (Pl. 91, fig. 2) represents an unseparated pinnule with 2–3 veins arising jointly from the mid rib far below the projection of the margin. The distance between two marginal projections represents the length of a pinnule.

Remarks. This species was first described and illustrated by Johnston (1887; 1888, pl. 26), and subsequently by Walkom (1925a, pp. 79–81, figs. 6–8). Townrow (1957) was doubtful about the propriety of referring two specimens, represented by Walkom's figs. 6 and 7, to this species, apparently because of some differences in the outline of the leaves. However, it is apparent from the specimens described above that the margins may vary even in the same leaf, and there is no doubt that Walkom's three specimens belong to this species.

Geinitz (1876, p. 6, pl. 2, figs. 7, 8) described the species *Pachypteris stelzneriana*, which Frenguelli (1941a) later redescribed as *D. stelznerianum*. Geinitz's drawings suggest that it is distinct from *D. coriacium*, but subsequent illustrations and a restoration of this species by Frenguelli (1941a) make it impossible to distinguish it from *D. coriacium*. If Frenguelli correctly identified his specimens with Geinitz's then the two species are in reality one.

Genus *PTERUCHUS* Thomas 1933

Pteruchus rhaetica (Geinitz) comb. nov.

Plate 90, fig. 15

1876 *Sphenolepis rhaetica* Geinitz, p. 12, pl. 2, figs. 23, 24.

1903 *Stachyopitys* sp., Seward, pp. 66, 67, pl. 9, figs. 1, 2.

Material. A single specimen (1136) consisting of a large number of microsporangiate (?) appendages arranged in fertile heads of c. 5 mm. in diameter. Stalks are not visible in the specimen, but the presence of more than one fertile head is clearly indicated.

Remarks. The specimen described above is specifically identical with *Sphenolepis rhaetica* Geinitz, whatever it may be. Geinitz (1876) had considered these fossils as spherical or compressed cones bearing numerous spirally arranged obovate woody scales. Seward (1903) considered them as male flowers. Although no spores have been recovered from the specimen, it seems to be an organ similar to microsporangiate structures described by Thomas (1933) as a species of *Pteruchus* Thomas.

Pteruchus is a pollen-bearing genus reminiscent of *Crossotheca*, a Palaeozoic pteridosperm microsporangiate structure (Delevoryas 1962, p. 123). Apparently similar Mesozoic microsporangiate fructifications have been referred to *Antholithus* (Antevs 1914) and *Stachyopitys* (Shirley 1898; Seward 1903), but these genera either lack a precise definition or include more than one natural group of plants (Thomas 1933). *Pteruchus*, on the other hand, is a precisely defined genus of *Corystospermaceae*, a family of Southern

EXPLANATION OF PLATE 91

Figs. 1, 2. *Dicroidium coriacium* (Johnston) Townrow. 1, 1089, almost three complete fronds, $\times 1$; 2, 1090, distal part of a frond with crenate margin, $\times 1$.

Figs. 3–7. *Xylopteris rigida* (Dun) comb. nov. 3, 1070, showing greater part of a frond, $\times 1$; 4, 1078, frond with closely arranged pinnules, $\times 1$; 5, 1075, $\times 1$; 6, 1126, indicating half a frond with distantly arranged pinnules, $\times 1$; 7, 1077, a smaller frond, $\times 1$.



Hemisphere pteridospermous plants. Therefore, the specimen described above is referred to this genus.

Genus FERUGLIOA Frenguelli 1944b

Feruglia samaroides Frenguelli (1944b)

Plate 97, figs. 15–19

Material. Two specimens (1064, 1105). 1064 (Pl. 97, figs. 15–17) measures *c.* 5.5 mm. in length and in width. It matches Frenguelli's specimen closely except that at the distal end it is apparently less cordate in shape, and the bifid micropyle is not as evident as in Frenguelli's specimen. The central line is also not very clear. The wing-like extensions are clearly seen.

1105 (Pl. 97, figs. 18, 19) is *c.* 6 mm. in length, and 4 mm. in breadth. It has a long distal prolongation, but the bifid nature of the micropyle is not evident. Wings are masked by the dark colour of the specimen; the central line is quite distinct.

Genus XYLOPTERIS Frenguelli 1943a

Xylopteris rigida (Dun) comb. nov.

- 1889 *Sphenopteris elongata* Carruthers; Szajnoch, pp. 223, 224, pl. 2, fig. 2.
- 1903 *Stenopteris elongata* (Carruthers) Seward, p. 70, pl. 7, fig. 2; pl. 11, fig. 3.
- 1909 *Stenopteris rigida* Dun, p. 313, pl. 50, figs. 1, 2.
- 1917a *Stenopteris elongata* (Carruthers) Walkom, p. 40, pl. 1, fig. 1; pl. 6, fig. 2.
- 1933 *Stenopteris densifolia* Thomas, p. 247, fig. 51.
- 1943b *Xylopteris elongata* (Carruthers) Frenguelli, pp. 324, 325, figs. 30, 31.
- 1951 *Xylopteris elongata* (Carruthers) Frenguelli; Menendez, pp. 224–6, pl. 15, figs. 9, 11.

Material. Ten fairly well-preserved specimens (1063, 1070–3, 1075–9, 1102). The largest is *c.* 10 cm. in length and no stalk is present in any. Typically, the main axis of each frond is forked once; each half regularly bears alternate to sub-opposite, simple, linear pinnae. Each pinna is *c.* 1 mm. broad, has a lamina with an entire margin, and, like the rachis, a single vein which terminates within a small rounded obtuse apex. The pinnae are spaced *c.* 0.5–1 cm. apart.

Remarks. This species has often been confused with *X. elongata* (Carruthers) Frenguelli (Carruthers 1872; Frenguelli 1943b). The latter has forked fronds, which are irregularly pinnate and have simple, forked, or more divided pinnae, often all on the same frond. *X. rigida*, on the other hand, has only simple and regularly arranged pinnae.

Further, it is difficult to distinguish between this species and *Xylopteris argentina* (Kurtz) Frenguelli (1943b). The latter is a rather ill-defined species based on some fragmentary specimens illustrated by Kurtz (1921, pl. 16, figs. 200–2). All these fragments may belong to *X. elongata* (Carruthers) Frenguelli, *X. rigida* (Dun) comb. nov., or *Sphenobaiera tenuifolia* (Johnston) comb. nov. (described later).

Considering the range of variation in size and spacing of the pinnae in *X. rigida*, it also becomes difficult to separate this species from *X. densifolia* (Du Toit) Frenguelli (Du Toit 1927, p. 364, text-fig. 13; Thomas 1933, text-fig. 51; Frenguelli 1943b).

Genus FANEROTHECA Frenguelli 1944a

Fanerotheca extans Frenguelli (1944b)

Plate 90, figs. 11–13

Material. A single specimen (1099, Pl. 90, fig. 12) having the appearance of a small flower-like structure

with four or more appendages terminating a small stalk. The terminal part of this fructification is c. 1 cm. in diameter. Also included in this species are specimens illustrated in Pl. 90, figs. 12, 13, printed from the old negatives left by Wieland, and for which the original specimens are no longer available.

Order CYCADEOIDALES, Family?
Genus YABEIELLA Oishi 1931

Yabeiella wielandi Oishi

Plate 92, figs. 1-7

- 1921 Un-named specimens, Kurtz, pl. 21, figs. 187, 190, 191, and the un-numbered figure to the left of 187.
1929 Un-named specimen, Wieland, p. 447, leaf in fig. 5a.
1931 *Yabeiella wielandi* Oishi, pp. 263, 264.
1943a *Yabeiella brackebushiana* (Kurtz) Oishi; Frenguelli, pl. 2, fig. 4.
1947 *Yabeiella brackebushiana* (Kurtz) Oishi; Jones and de Jersey, pp. 50, 51, text-figs. 43, 45.

Material. Five specimens (1008?, 1026-8, 1030). Holotype (1026, Pl. 92, figs. 1-2) is c. 3.1 cm. in length, 0.8 cm. in width. The margin, as in all other specimens of this genus, is entire. It has parallel sides and an obtusely rounded apex. Lateral veins form angles of about 65° with the mid rib. Some of the lateral veins fork once at varying distances from the mid rib, while some unite with the adjoining ones. Near the margin of the leaf there are about 18 lateral veins per cm., and all of them join the marginal veins. In 1027 (Pl. 92, fig. 3) the apex of the leaf is more or less acute. 1028 (Pl. 92, figs. 4, 5) has a narrower form, c. 5.5 mm. in width. 1008 (Pl. 92, figs. 6, 7) is the largest specimen, c. 8.8 cm. in length, but having much fewer and steeper lateral veins (about 11-13 per cm. along the margin, and forming angles of about 45° with the mid rib); no cross connexions between the veins are visible; the general form of the leaf is like that of the other specimens, but this specimen is only tentatively assigned to the species.

Remarks. There is a considerable range of variation in form and venation of the leaf. Further, although a large number of specimens have been assigned to this species, nothing is known about the base of the leaf.

Jones and de Jersey (1947) are of the opinion that this species is indistinguishable from *Yabeiella brackebushiana*, and that the specimens referred to it show secondary veins identical with those of *Y. brackebushiana*; however, the leaves have rounded apices, and have parallel edges, in contrast to the acute apex and lanceolate form of the latter. Further, they think that Kurtz's specimens demonstrate a gradation in the acuteness of the apices and in the form of the leaves.

On the contrary, *Y. wielandi* is easily distinguishable from *Y. brackebushiana*, even if the apices are not quite rounded in the former. There is a consistent difference in the shape and in the lateral veins of the leaves of the two species, and there is no indication that the specimens are fragments of compound leaves. All the available specimens strongly indicate that they are fragments or whole specimens of simple leaves.

EXPLANATION OF PLATE 92

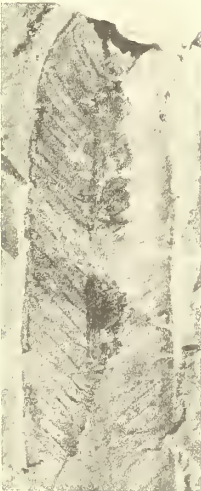
- Figs. 1-7. *Yabeiella wielandi* Oishi. 1, 1026, holotype, also with the holotype of *Fraxinopsis major* Wieland, $\times 1$; 2, holotype, showing details, $\times 2.5$; 3, 1027, a fragment with more or less acute apex, $\times 1$; 4, 1028, a narrower form of leaf, $\times 1$; 5, same, showing details, $\times 2.5$; 6, 1008, leaf with fewer and steeper veins, $\times 1$; 7, same, showing details, $\times 2.5$.
Figs. 8-14. *Yabeiella spatulata* Oishi. 8, 1062, $\times 1$; 9, same, showing details, $\times 2.5$; 10, 1021, a small complete leaf, $\times 1$; 11, 1022, $\times 1$; 12, same, showing details, $\times 2.5$; 13, part of 1019 showing veins, $\times 2.5$; 14, 1032, basal part of a leaf, $\times 1$.



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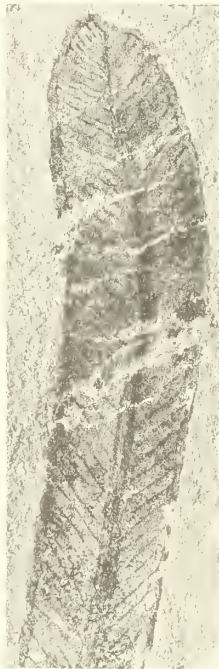
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Yabeiella spatulata Oishi

Plate 92, figs. 8–14

1931 *Yabeiella spatulata* Oishi, p. 264, pl. 26, figs. 2, 2a.1947 *Yabeiella brackebushiana* (Kurtz) Oishi; Jones and de Jersey, text-figs. 43, 46.

Material. Eight specimens (1018–23, 1031, 1062), up to 6.5 cm. in length, and 7 mm. in width at the apex. The leaf is shortly petiolate to sub-sessile at the base, and gradually wider toward the apex (being more so in smaller or younger specimens). When present, the apex appears to be emarginate. The mid rib is characteristically stout up to the apex, longitudinally striated, and minutely pitted. The lateral veins form angles of about 55–65° with the mid rib, fork once at some distance from the mid rib (a few unite with the adjoining ones), and number 11–14 per cm. along the margin of the leaf before they unite with the marginal vein.

Remarks. Oishi (1931) founded this species on a single specimen from the Triassic of Argentina, in which the leaf has a broad, rounded apex. In the specimens described above, only two show apices, which are emarginate. An emarginate apex may be a character of the species, or it may result from some injury while the leaf was young; therefore, this character alone is insufficient to assign these specimens to a new species. All other characters are identical with the previously known characters of this species.

Yabeiella brackebushiana (Kurtz) Oishi

Plate 93, figs. 1–5

1921 *Oleandridium brackebushianum* Kurtz, pl. 18, fig. 307; pl. 21, figs. 147–50, 302, 304–6 (also un-named figs. in same plate, 145, 310, 312).1927 *Taeniopteris* cf. *brackebushiana* (Kurtz) Du Toit, p. 354, text-fig. 2.1931 *Yabeiella brackebushiana* (Kurtz) Oishi, p. 263, pl. 26, figs. 3, 5, 6.

Material. Three specimens (1007, 1009, 1029), up to 12 cm. in length, and 1.6 cm. in width in the middle. The mid rib is thick at the base, becoming gradually narrow above. Lateral veins form angles of 60–70° with the mid rib (angles being smaller at the apex and the base). Only a few veins are seen to bifurcate once and unite with the adjacent veins at different distances away from the mid rib. There are about 20 veins per cm. along the margin.

Remarks. *Y. brackebushiana* is a species with rather variable characters. It includes leaves with acute to acuminate apices, veins ranging from 14–20 per cm. along the margin, and forming angles of 50–70° with the mid rib. The specimens described above are similar to Kurtz's figs. 145, 308, and 312.

Yabeiella crassa Jones and de Jersey

Plate 93, figs. 6–13

1947 *Yabeiella crassa* Jones and de Jersey, pp. 53, 54, text-fig. 48, fig. 5 (only).

Material. Four specimens (1011, 1013 a, b, 1016), up to 7 cm. in length, and up to 1.6 cm. in width. The leaf has sub-sessile base, and narrowly obtuse apex. Mid rib is generally thick and distinctly striated, c. 2 mm. toward the base. Lateral veins form angles of about 65° with the mid rib, being somewhat steeper toward the apex, and number about 14 per cm. along the margin. Forking and union of veins are rare.

Remarks. The specimens generally agree with those of Jones and de Jersey (1947), who

have also included in this species some fragments of much larger leaves which apparently belong to *Y. mareyesiaca*.

Yabeiella mareyesiaca (Geinitz) Oishi

Plate 94, figs. 1-6

- 1876 *Taeniopteris mareyesiaca* Geinitz, p. 9, pl. 2, figs. 1-3.
 1917a *Taeniopteris dmstoni* Walkom, p. 37, pl. 9, fig. 1.
 1921 *Oleandridium mareyesiacum* (Geinitz); Kurtz, pl. 21, figs. 189, 314a.
 1931 *Yabeiella mareyesiaca* (Geinitz); Oishi, pp. 262-3.
 1947 *Yabeiella crassa* Jones and de Jersey, p. 53, pl. 8, fig. 1.

Material. Four incomplete specimens (1010, 1012, 1014-15), up to 7.5 cm. in length, and 2 cm. in width below the apex. Lateral veins form angles of 70-75° with a narrow mid rib. Some of the lateral veins fork once, and a few others unite with adjacent veins. They number 18-20 per cm. along the margin of the leaf.

Remarks. The specimens generally agree with those illustrated by Geinitz (1876) and Kurtz (1921). It is unfortunate, however, that Geinitz described the lateral veins as forming angles of about 85° with the mid rib, while his illustrations show angles of only 70-75°.

Yabeiella sp. indet.

1024 (Pl. 94, figs. 8-10) shows the greater part of a probably immature leaf without its apex. It is c. 2.8 cm. in length, and c. 7 mm. in width slightly above the base. The mid rib is somewhat thick at the base and narrow above. Lateral veins form angles of about 60-70° with the mid rib, and number about 24 per cm. near the marginal vein. Some of the lateral veins fork, and a few unite with the adjacent ones. Although the leaf has rather well defined characters, the small size and frequency of lateral veins per unit length of the leaf suggest that it is probably an immature leaf. Thus, it is not possible to assign it to any of the species described above.

1025 (Pl. 94, figs. 11, 12) is complete, shortly petiolate, c. 3.7 cm. in length (including a petiole c. 1 cm. long) and c. 6 mm. in width below the apex. It has a relatively thick mid rib, which remains equally thick up to the apex. The lateral veins form angles of about 65-70° with the mid rib; some of them fork once, and a few unite with the adjacent ones. They number about 20 per cm. near the marginal veins. This also is an apparently immature leaf. The thick mid rib, somewhat spatulate shape, and

EXPLANATION OF PLATE 93

- Figs. 1-5. *Yabeiella brackebushiana* (Kurtz) Oishi. 1, 1007, an almost complete leaf, $\times 1$; 2, part of above showing details of venation, $\times 2.5$; 3, 1029, a fragment with short acute apex, $\times 1$; 4, 1009, $\times 1$; 5, 1009, showing venation in the apex, $\times 2.5$.
 Figs. 6-13. *Yabeiella crassa* Jones and de Jersey. 6, 1011, sub-basal region of a leaf, $\times 1$; 7, part of above showing venation, $\times 2.5$; 8, 1016, basal part of a leaf, $\times 1$; 9, same, showing details, $\times 2.5$; 10, 1013a, $\times 1$; 11, same, showing veins, $\times 2.5$; 12, 1013b with apical part of a leaf, $\times 1$; 13, same, enlarged to show veins, $\times 2.5$.

EXPLANATION OF PLATE 94

- Figs. 1-7. *Yabeiella mareyesiaca* (Geinitz) Oishi. 1, 1014, leaf with sub-sessile base and missing apex, $\times 1$; 2, part of 1014 showing details, $\times 2.5$; 3, 1010, indicating apex, $\times 1$; 4, details of venation in the apex, $\times 2.5$; 5, 1015, showing middle part of a distorted leaf, $\times 1$; 6, part of 1015 with details of venation, $\times 2.5$; 7, 1012, a fragment with sub-sessile base, $\times 1$.
 Figs. 8-12. *Yabeiella* sp. 8, 1017, $\times 2.5$; 9, 1024, an immature leaf, $\times 1$; 10, same, with details of venation, $\times 2.5$; 11, 1052, another immature leaf, $\times 1$; 12, same, showing veins, $\times 2.5$.



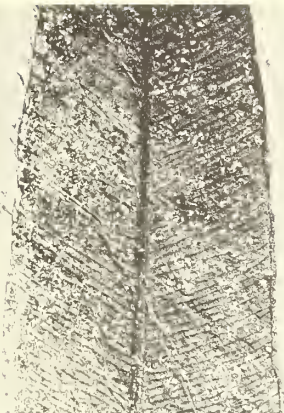
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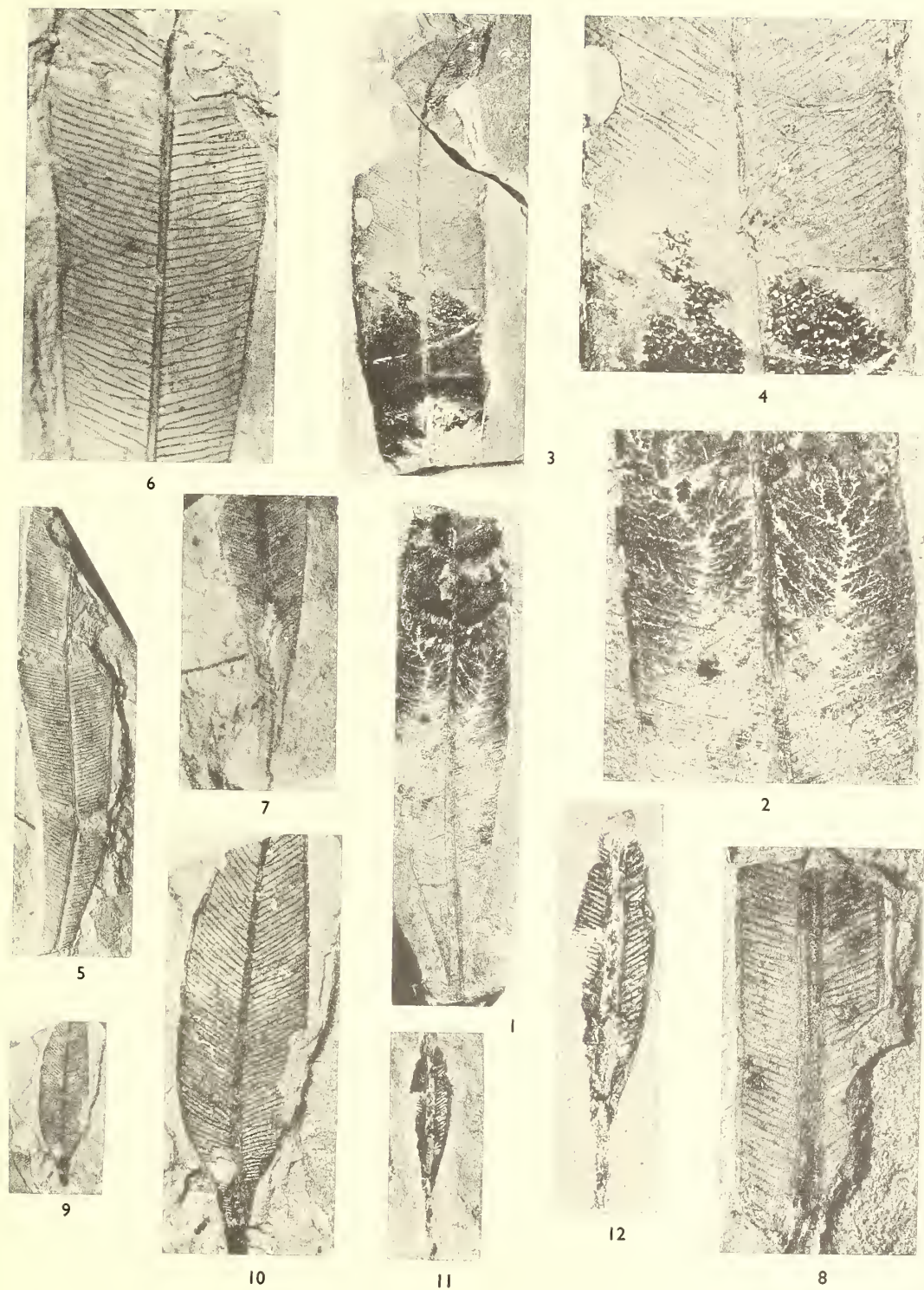
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frequency of lateral veins suggest that it may belong to *Y. spatulata*, but without intermediate forms identification is uncertain.

1017 (Pl. 94, fig. 8) shows the middle part of a leaf. It is *c.* 4 cm. in length, and *c.* 9 mm. in width, with almost parallel edges, a thick, longitudinally striated mid rib, and numerous (about 24 per cm). lateral veins arising from the mid rib at angles of about 65°. Some of the lateral veins fork once, and a few join the adjacent ones. This specimen shows some resemblance to *Y. wielandi*, particularly in having parallel edges, and in the narrow form of the leaf, but it obviously differs from that species in having a thick mid rib, and numerous veins (about 24 per cm. as against 14–18 in that species). It is not impossible that this specimen shows an extreme form of *Y. wielandi*, and may actually belong to it.

Class CONIFEROPHYTA

Order GINKGOALES

Family GINKGOACEAE

Genus BAIEROPHYLLITES gen. nov.

Type species. *B. florinii* sp. nov.

Generic diagnosis. Same as for the type species, see below.

Baierophyllites florinii gen. et sp. nov.

Plate 95, figs. 1–5; Plate 96, figs. 1–3

Diagnosis. Leaves narrow, linear, up to 13 cm. long and 0.5 cm. broad, without any distinction into petiole and lamina, forked only once at some distance above the base into more or less equal halves that terminate in round or somewhat depressed apices; veins indistinct.

Cuticle moderately thick, epidermal cells rectangular over the veins, shorter further away, with straight walls; stomata scattered sparsely in vein and intervein areas, each typically having two small terminal, and two large lateral subsidiary cells; lateral subsidiary cells over the veins scarcely or little different from the ordinary epidermal cells, but forming a more or less round group of cells in stomata away from the veins; no papillae on epidermal or subsidiary cells.

Description. Four specimens (1083–4, 1086, 1120). The holotype, 1120 (Pl. 95, figs. 1–5) shows a few overlapping leaf compressions. The form of the leaf is better seen in other specimens, but this specimen is significant in having cuticle preserved in places. Although the veins are not clearly visible in the specimens, they are more easily recognized in the cuticle. Because of the small size of cuticle pieces, however, the number of veins could not be determined.

The cuticle is moderately thick, the epidermal cells are rectangular, *c.* 120–50 μ long and 20–25 μ broad over the veins, and shorter and irregular away from the veins. They have straight walls and no papillae. The stomata are thinly scattered over the entire leaf surface. Along the veins the stomata are typically longitudinally oriented, i.e. the axes of the stomatal apertures are parallel with the long axis of the leaf. The stomatal aperture is narrow, *c.* 25 μ long, and flanked by a pair of guard cells which are nearly as long as, or a little longer than, the aperture. Guard cells (Pl. 95, figs. 4, 5) are *c.* 7 μ wide in the middle but are abruptly narrowed to a line on either end. Each stoma has a short terminal subsidiary cell at either pole. A large subsidiary cell is adjacent to each

guard cell. These lateral subsidiary cells are scarcely different from the adjoining epidermal cells, except for a slight difference in size.

The stomata have the same fundamental structure away from the mid rib except that they appear to be surrounded by a group of two to five, usually four, subsidiary cells. This is apparently due to divisions of the lateral subsidiary cells or polar epidermal cells, or both. The stomatal apparatus is also a little wider than it is over the veins.

Only in one widely open, and particularly well-preserved, stoma (Pl. 95, fig. 3) was it possible to see that a cuticular flap formed a sort of arch over the stomatal aperture, leaving only a small stomatal passage. In the figure the flap is seen as a lighter area on the inner sides of the guard cells enclosing a slit-like stomatal aperture.

1084 (Pl. 96, fig. 1) shows a poorly preserved leaf of full size. It also shows the place and extent of forking and a depressed apex in one of the halves.

Remarks. The specimens have been referred to a new genus of Ginkgoaceae. The form of the leaf and the cuticular structures amply support this assignment. The genus is probably closer to *Ginkgoites* than to *Sphenobaiera*. Some affinities with *Sphenobaiera* are indicated by the form, but the cuticular structure of species of *Sphenobaiera* (Harris 1935; Florin 1936 *a, b*; Kräusel 1943) indicates the fundamental difference between the two genera. The subsidiary cells around the guard cells in the cuticles of *Sphenobaiera* show a varying degree of development of papillae projecting over the guard cells, a character entirely absent in the new genus. This character, as well as the presence of small terminal subsidiary cells, indicates closer affinities with *Ginkgoites* (Harris 1935).

Genus SPHENOBAIERA Florin 1936a

Sphenobaiera argentinae (Kurtz) Frenguelli

Plate 96, figs. 4, 5

1876 *Baiera taeniata* Geinitz, p. 8, pl. 2, fig. 10.

1894 *Baiera argentinae* Kurtz, pl. 4, figs. 4-6.

1946 *Sphenobaiera argentinae* (Kurtz) Frenguelli, pp. 109-19, pl. 2, fig. 4; pl. 3; pl. 4, figs. 1, 2; pl. 5; pl. 6, fig. 1.

EXPLANATION OF PLATE 95

Figs. 1-5. *Baierophyllites florinii* gen. et sp. nov. Holotype, 1120. 1, leaves, $\times 1$; 2, cuticle from area away from veins, $\times 100$; 3, stoma from cuticle away from vein, $\times 500$; 4, cuticle on the vein, $\times 100$; 5, stoma from cuticle on the vein, $\times 500$.

EXPLANATION OF PLATE 96

Figs. 1-3. *Baierophyllites florinii* gen. et sp. nov. 1, 1084, a complete leaf, $\times 1$; 2, 1086, another leaf with almost swollen ends, $\times 1$; 3, 1083, a smaller leaf showing depressed tips of each half of the leaf, $\times 1$.

Figs. 4, 5. *Sphenobaiera argentina* Frenguelli. 4, 1056, showing major part of a leaf, $\times 1$; 5, a part of a segment of the above showing veins, $\times 2.5$.

Figs. 6-9. *Sphenobaiera tenuifolia* (Johnston) comb. nov. 6, 1080, greater part of a leaf with double dichotomy, $\times 1$; 7, 1081, a leaf with triple dichotomy, $\times 1$; 8, 1082, a fragment with double dichotomy, $\times 1$; 9, 1074, stem with attached leaves, $\times 1$.

Fig. 10. *Baiera rollerii* Frenguelli. 1122, $\times 1$.

Fig. 11. *Baiera cuyana* Frenguelli. 1121, $\times 1$.

Figs. 12, 13. *Stachyopitys anthoides* Frenguelli. 12, 1110, $\times 1$; 13, same, enlarged, $\times 2.5$.



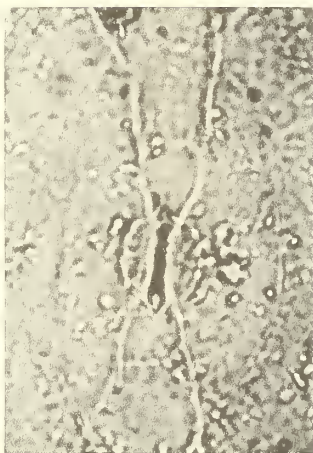
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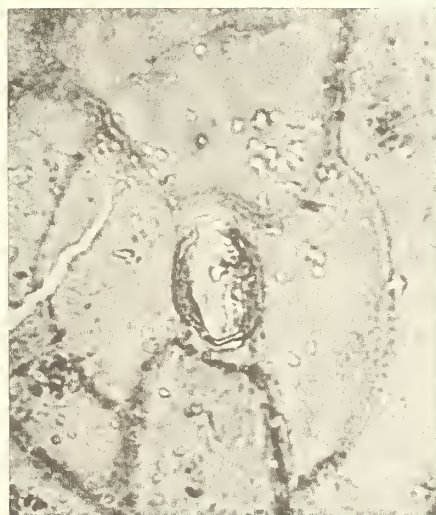
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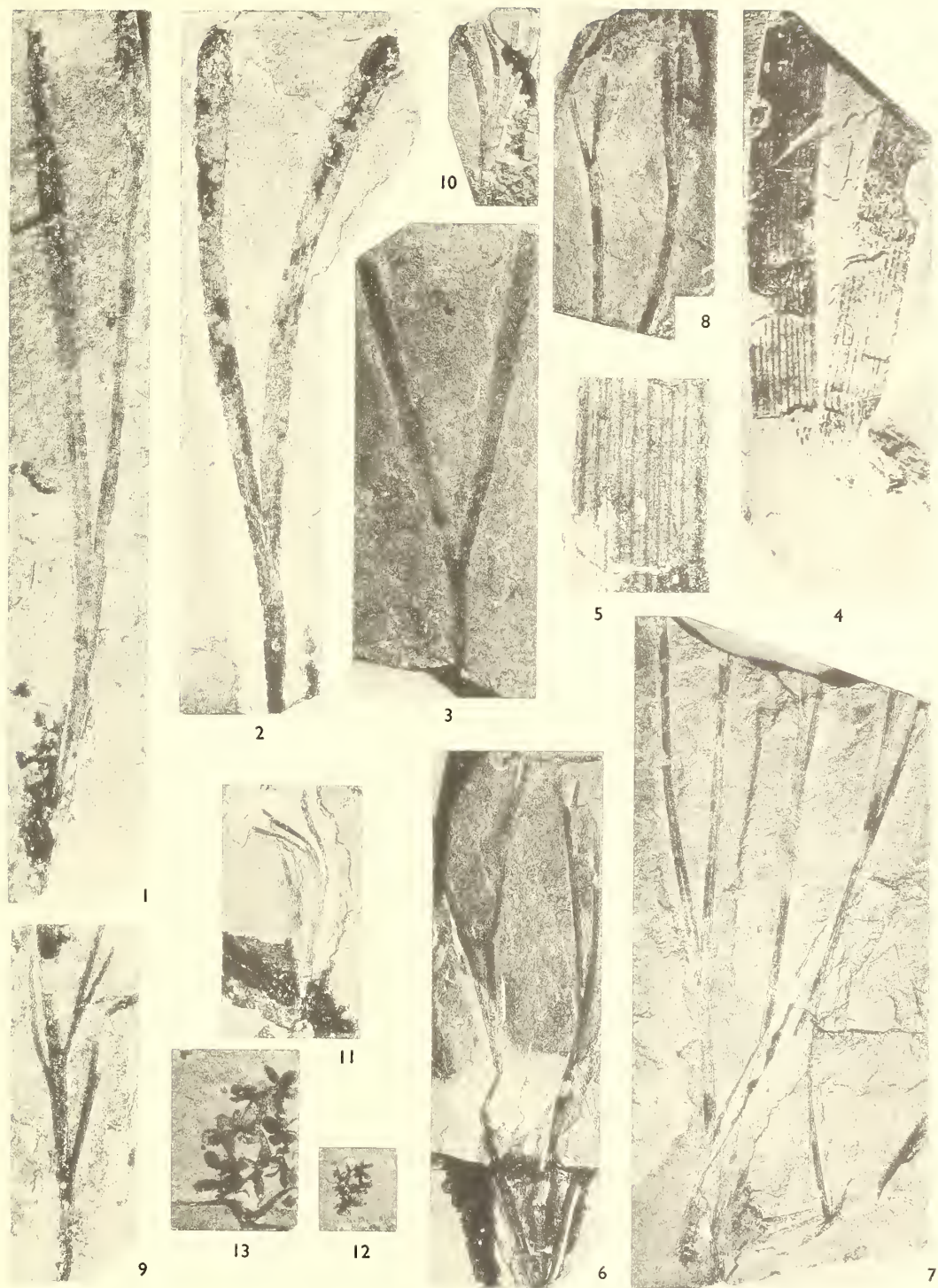
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Material. A single specimen (1065), c. 8.5 cm. in length, is distally forked once. Each segment of the fork is c. 1 cm. in width, and shows about 10 parallel veins.

Remarks. This species resembles *Sphenobaiera longifolia* (Heer 1876, pl. 7, figs. 2, 3; pl. 8), but differs essentially in having only once-forked leaves.

Sphenobaiera tenuifolia (Johnston) comb. nov.

Plate 96, figs. 6-9

1887 *Baiera tenuifolia* Johnston, p. 176, pl. 3, figs. 2 a-e.

1890 *Trichopitys johnstonii* Feistmantel, p. 113.

1947 *Czekanowskia tenuifolia* (Johnston) Jones and de Jersey, pp. 59-61, text-fig. 55; pl. 5, fig. 4?; pl. 6, fig. 2.

Material. Five specimens (1080-2, 1074, 1103), up to 10 cm. in length, and each segment c. 1-1.5 mm. in width. The leaf is in the form of a two-dimensional axis which is two to three times dichotomously branched. A single longitudinally striated vein is seen throughout the leaf.

1074 (Pl. 96, fig. 9) is a stem fragment bearing bases of three leaves, one of the latter showing a distinct dichotomy, another one also indicating a dichotomy with a small base of a missing branch of the leaf. The axis is c. 3 mm. in width, suggesting that it represents a young part of the stem.

Remarks. This species was previously known only from the Triassic of Tasmania. It shows some resemblance to *Czekanowskia* and *Trichopitys* on the one hand, and *Sphenobaiera* on the other. Feistmantel (1890) referred this species to *Trichopitys* on the assumption that certain fructifications found in close association with these leaves were very like those found in the genus. But Walkom (1925a) failed to find any actual connexion between fructifications and leaves, and no such fructifications have been found in association with the specimens described above. It is therefore reasonable not to refer to these leaves as *Trichopitys*.

The leaves show some resemblance to *Czekanowskia* Heer in form, but there is no evidence to show that they were born in clusters or on dwarf shoots. Further, the cuticular structure of this species described by Jones and de Jersey (1947) is quite unlike that of *Czekanowskia*, particularly in having prominent epidermal papillae, hitherto unknown in *Czekanowskia*. If specimen 1074 (Pl. 96, fig. 9) represents the kind of plant that produced these leaves, as has been supposed here, the evidence is that these leaves were borne singly. There is thus no sound basis for referring this species to *Czekanowskia*.

On the other hand, the morphology and cuticular structures suggest affinities with *Sphenobaiera* Florin, particularly *S. furcata* (Heer) Florin (Kräusel 1943, text-figs. 9, 10). However, it differs specifically from the latter at least in lacking the terminal dichotomy of the segments of the leaves. It is therefore included in this genus as *Sphenobaiera tenuifolia* (Johnston) comb. nov.

Genus BAIERA Braun 1843

Baiera rollerii Frenguelli (1946)

Plate 96, fig. 10

Material. A single specimen (1122), a poorly preserved whitish impression on a light piece of rock. It is c. 2.3 cm. in length, and c. 0.3 cm. in width at the undivided widest part of the wedge-shaped leaf.

Distally it is divided into four segments, each of which is nearly as long as the undivided basal part of the leaf. No veins are visible.

Baiera cuyana Frenguelli (1942)

Plate 96, fig. 11

Material. A single specimen (1121), *c.* 3.5 cm. in length, and roughly wedge-shaped with a small stalk, and a distally divided lamina. The lamina is divided into six segments; a deep central incision divides the distal segments into two groups of three each. Preservation is poor, and no veins are visible.

Remarks. This species is distinguishable from *B. rollerii* Frenguelli in having a central long incision dividing the lamina into two primary lobes, each in turn being divided into three segments, as opposed to three equally deep incisions dividing the lamina into four equal segments in *B. rollerii*.

Genus PHOENICOPSIS Heer 1876

Phoenicopsis elongatus (Morris) Seward

Plate 97, figs. 1, 2

1927 *Phoenicopsis elongatus* (Morris) Seward; Du Toit, p. 368.

1947 *Phoenicopsis elongatus* (Morris) Seward; Jones and de Jersey, p. 62, text fig. 57.

1951 *Podozamites elougatus* (Morris) Feistmantel; Menendez, p. 206, pl. 12, fig. 5.

Material. Three specimens (1068, 1131–2), up to 11 cm. in length, and 0.7 cm. in width. The leaf gradually tapers at one end, where it measures *c.* 4.5 cm. in width. There are about 13–14 simple veins separated from each other by narrow 'interstitial veins'.

Remarks. This species has been shuffled between *Podozamites* and *Phoenicopsis*, mainly because it was based on isolated leaves that can hardly be distinguished from the dispersed leaves of *Podozamites*. Also, many specimens have been found from various localities showing their occurrence in fan-shaped dwarf shoots. On the other hand, no specimen has so far been recorded showing the attachment of these leaves along an elongated axis that would indicate their affinity with *Podozamites*. It seems reasonable to assign this species to *Phoenicopsis* Heer.

EXPLANATION OF PLATE 97

Figs. 1, 2. *Phoenicopsis elongatus* (Morris) Seward. 1, 1068, a leaflet, $\times 1$; 2, part of above showing veins, $\times 2.5$.

Figs. 3, 4. *Incertae sedis*. 3, 1134, $\times 2$; 4, 1135, $\times 1$.

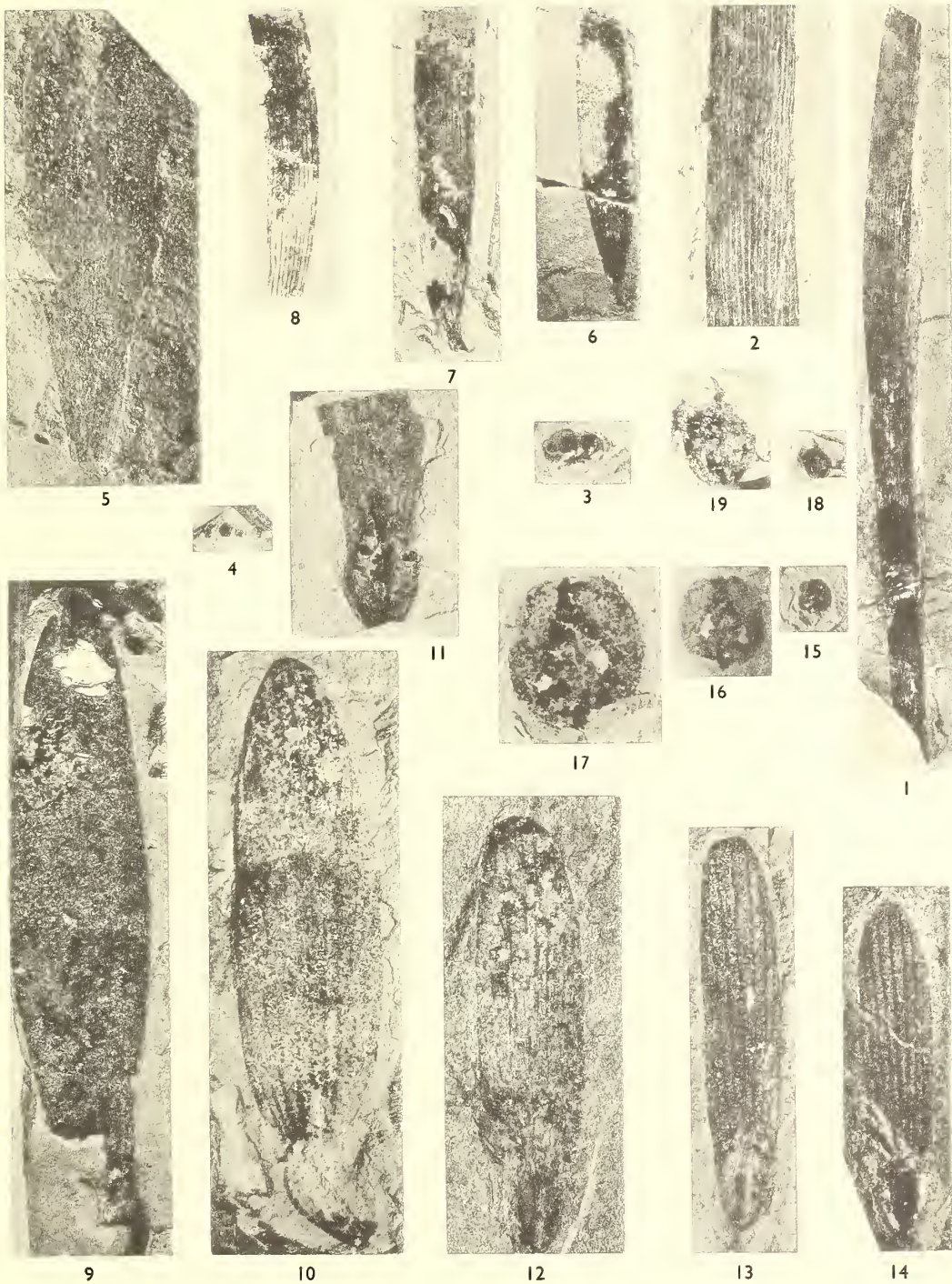
Fig. 5. *Noeggerathiopsis* sp., 1098, $\times 1$.

Figs. 6–8. *Podozamites lanceolatus* var. *geminus* Heer. 6, 1087, a small complete leaflet, $\times 1$; 7, 1066, greater part of a larger leaflet, $\times 1$; 8, 1076, a fragment showing veins, $\times 1$.

Figs. 9–11. *Fraxinopsis major* Wieland. 9, 1061, the largest specimen incomplete at the base, $\times 2.5$; 10, holotype, 1033, $\times 2.5$; 11, 1042, basal part indicating the complete division of the basal body into two equal halves, $\times 2.5$.

Figs. 12–14. *Fraxinopsis minor* Wieland. 12, 1034, lamina with one forking vein, $\times 2.5$; 13, 1032, a specimen with narrower lamina, $\times 2.5$; 14, 1039, a smaller specimen with narrow lamina, $\times 2.5$. Note the absence of forked veins in figs. 13, 14.

Figs. 15–19. *Feruglioia samaroides* Frenguelli. 15–17, 1064; 15, $\times 1$; 16, $\times 2.5$; 17, $\times 5$. 18, 19, 1105; 18, $\times 1$; 19, $\times 2.5$.



Genus STACHYOPTYIS Schenk 1867

Stachyopitys anthoides Frenguelli (1944a)

Plate 96, figs. 12, 13

Material. A single specimen (1100), c. 7 mm. in length, and c. 5 mm. in width, appearing as a small axis bearing alternately arranged, minute bodies, looking like tiny flowers. Each body consists of 4–5 small oval appendages.

Order CORDAITALES

Family CORDAITACEAE

Genus NOEGGERATHIOPSIS Feistmantel 1879

Noeggerathiopsis sp.

Plate 97, fig. 5

Material. A single badly preserved specimen (1098). It is an elongate-spatulate leaf with a rounded apex that appears parted in the middle, perhaps due to faulty preservation, or to injury. It is c. 6.5 cm. in length, and c. 2.1 cm. in width below the apex, tapering gradually to a 6 mm. wide base. The veins are barely visible.

Remarks. The specimen shows considerable resemblance to *Noeggerathiopsis hislopi* (Bunbury) Feistmantel in shape, but the species of this genus are better distinguished from each other with the help of cuticular structures.

Because of the striking resemblance between the leaves of this genus and of *Cordaites* Unger, there has been a persistent suspicion that the two genera are, in reality, one. Pant and Verma (1964) have demonstrated similarity in the cuticular structure of these genera and have further emphasized the possibility of generic identity. However, they have preferred to retain *Noeggerathiopsis* as a distinct genus.

Order CONIFERALES, Family?

Genus PODOZAMITES (Brongn.) Braun 1843

Podozamites lanceolatus var. *genuinus* Heer (1876)

Plate 97, figs. 6–8

Material. Four poorly preserved specimens (1066–7, 1087, 1133), measuring 4.1–5.7 cm. in length, and 0.7–0.9 in width near the spatulate apex. There are 8–11 indistinct veins converging towards the narrow base of the leaf.

Order CONIFERALES, Family?

Genus FRAXINOPSIS Wieland 1929

Fraxinopsis major Wieland

Plate 97, figs. 9–11

1929 *Fraxinopsis major* Wieland, pp. 447–8, fig. 5a.1944c *Cycadocarpidium majus* Frenguelli, pp. 557–8, pl. 3.

Material. Five specimens (1033, 1042–3, 1051, 1069). The holotype (1033, Pl. 97, fig. 10) has apparently deteriorated considerably since it was studied by Wieland (1929). The veins have almost disappeared in the basal part of the lamina. It measures c. 3.5 cm. in length including its basal fertile

part, which has a body, or possibly two, separated from each other by a distinct longitudinal slit. The distal sterile part of the lamina has numerous veins that apparently fork more than once.

The largest specimen (1061, Pl. 97, fig. 9) is *c.* 3.5 cm. in length, excluding the basal fertile part of the sporophyll, which is largely missing.

Remarks. See remarks under *F. minor* below.

Fraxinopsis minor Wieland

Plate 97, figs. 12-14

1929 *Fraxinopsis minor* Wieland, pp. 447-8, fig. 5b.

1941b *Cycadocarpidium andium* Frenguelli, pp. 485-98, pl. 1-3.

1944c *Cycadocarpidium minus* Frenguelli, pp. 557-68, pl. 1-4.

Material. Fourteen specimens (1032, 1034-41, 1123-7), most of which are poorly preserved or fragmentary. They vary in size from 2-2.5 cm. in length including the basal fertile part, and 4-6.5 mm. in width. Typically there are seven simple veins in the distal sterile part of the lamina. In some of the wider specimens, one of the veins is seen to fork (Pl. 97, fig. 123). The basal fertile part is quite similar to that of the other species described above.

Remarks. Wieland (1929), reporting on these two species, described these fructifications as 'fruits', noting some resemblance between *Fraxinopsis* and *Cycadocarpidium* Nathorst, but considering them as distinct. Further, he favourably compared these fossils with fruits of the modern genus of angiosperms, *Fraxinus*, the source of the generic name *Fraxinopsis* Wieland.

Oishi (1931) described specimens of *F. minor* from the Cacheuta beds of the same formation, located a few miles away from Minas de Petroleo. He thought these fructifications did not belong to angiosperms, but were probably gymnosperms or 'hemiconifers' (of Wieland 1929). Seward (1931) also compared *Fraxinopsis* Wieland and *Cycadocarpidium* Nathorst, without giving any opinion about their relationship. Harris (1935) remarked on some resemblances among *Fraxinopsis* Wieland, *Cycadocarpidium* Nathorst, and *Dioonitocarpidium* Lilienstern, but allowed the possibility that they might be different genera.

Frenguelli (1941c), possibly unaware of *Fraxinopsis*, described some specimens as *Cycadocarpidium andium*. Subsequently Frenguelli (1944c) suggested differences between *C. andium* and *Fraxinopsis minor*, but considered *Fraxinopsis* and *Cycadocarpidium* generically identical, transferring species from the former to the latter.

Dioonitocarpidium (Lilienstern 1928) consists of an axis bearing two rows of sickle-shaped appendages, and, near the base of the axis, two small bodies, each about 1 cm. long. It is thus quite different from *Fraxinopsis*, in which there are no appendages at all. Similarly, *Cycadocarpidium* Nathorst is an alate organ having a distal sterile laminate part similar to that of *Fraxinopsis*, and a stalk-like basal part bearing a pair of appendages, each of the latter bearing a seed-like body. In *Fraxinopsis*, on the other hand, the basal fertile part is also more or less laminate in form, and has no appendages at all. Thus, structurally, *Fraxinopsis* is distinct from the other two genera.

Regarding the affinities of this genus, there is no evidence to support the view that it could belong to the angiosperms. It was the basal fertile part of the fructifications that Wieland (1929) considered to be seeds, showing the two cotyledons of their embryos. This, and the presence of some taeniopteroid leaves, which, he thought, were also of

angiosperms, led him to assign the fructifications to the angiosperms. Oishi (1931) noted that a clear space divides the basal body into two, and the two bodies only happen to lie very close to each other. This fact, and the apparent similarity between the sterile distal parts of these fructifications in this genus and *Cycadocarpidium*, suggest that there may be some affinity between the two genera.

Concerning the taxonomy of the genus, *Fraxinopsis minor* and *F. major* are distinct from each other, not only in size differences, but also in the profuse branching of the veins in the distal sterile part of the lamina in *F. major*, and the almost simple veins in the others. Also, it is interesting to note that the branching of veins in the lamina tends to coincide with the larger width of the specimens. It is quite possible, therefore, that the specimens assigned to *F. major* simply represent the largest specimens of one and the same species, *F. minor*. But this is purely speculation until other specimens are found to bridge the gap in the known characters of the two species.

On the other hand, it is impossible to distinguish between *F. minor* and the so-called *Cycadocarpidium andium*. The comparative data published by Frenguelli (1944c, p. 560) to demonstrate the distinction between them seem to emphasize the continuous range in size and other characters in the two species. Further, one specimen of *C. andium* is shown to have a forking vein in the distal lamina. This character, which obviously varies with the width of the lamina (Pl. 97, figs. 122–4), is not lacking in *F. minor* either. Therefore, *C. andium* Frenguelli would seem to be a later synonym of *F. minor*.

Incertae Sedis

Specimens 1128, 1129 (Pl. 90, figs. 9, 10). Both lie close together on the same rock fragment. 1128 shows a three-dimensional body terminating a small stalk. The terminal body shows three ovoid lobes, each c. 6 mm. in length, and up to 3 mm. in width. The other specimen shows a four-lobed structure, each with the same dimensions as in the first.

These specimens show superficial resemblance to *Sagenopteris nilssoniana* (Brongn.) Ward, in Frenguelli (1941c, pl. 3, figs. 4, 5), but no veins are visible in our specimens. The absence of veins and the three-dimensional appearance of the specimens suggest that these may be some sort of fructification, rather than the foliage of *Sagenopteris*. They also bear a striking resemblance to *Fanerotheca extans* Frenguelli (Pl. 90, figs. 42–44), but a precise comparison is impossible.

Specimen 1130 shows two seed-like bodies split open longitudinally into halves (Pl. 90, fig. 14). Each body is c. 5–7 mm. in length, and c. 3–4 mm. in width, showing a central part surrounded by a thick wall. No other details are visible. It is difficult to ascertain their natural affinities, but they have the appearance of seeds or fruits.

Specimen 1101 (Pl. 90, fig. 16) is a cluster of seed-like bodies attached to an axis by short stalks. Each body is a small ovoid structure, c. 2 mm. in long diameter, and a little shorter in the other. The axis is not entirely exposed, but attempts to expose it further would have ruined the specimen.

These bodies probably represent some kind of ovulate fructification. Apparently similar bodies are usually found associated with the leaves of ginkgophytes as well as certain pteridosperms, particularly the *Corystospermaceae* (Thomas 1933).

Specimens 1134, 1135. 1134 (Pl. 97, fig. 3) consists of a small laminate organ bearing three small bodies on its surface. The entire specimen measures c. 4×2 mm. The small bodies are of unequal size, c. 1 mm. in diameter, and each having a distinct border separated from a central mass by a distinct groove. 1135 (Pl. 97, fig. 4) is a more fragmentary specimen bearing four bodies on its surface.

It is difficult to ascertain the morphology and affinity of these specimens. They bear superficial resemblance to *Unkomasia cacheutensis* (Frenguelli 1942, p. 317, fig. 1).

CONCLUSIONS

Stratigraphy. The relationships of the four beds or 'Estratos' of the Cacheuta Formation with other Triassic beds of Argentina were reviewed and summarized by Groeber and Stipanovic (1952). They considered these beds to be of Norian to Rhaetic age (Table 1), perhaps allowing for the possibility that the Beds of Cerro de la Cabras may be a little older, i.e. of Upper Carnian, and that those of Rio Blanco may be a little younger than Rhaetic.

Krishnan (1954) also considered these beds to be mainly 'Upper Triassic', with the probability that the La Cabras may be partly 'Middle Triassic', and the Rio Blanco, Rhaetic. However, Frenguelli (1948) had reached the conclusion that these beds are 'Middle Triassic to Rhaetic', possibly even 'Lower Jurassic' in age. He had also compared the flora of the 'Estratos de los Rastros-Potreriillos' with the Middle Triassic floras of Africa and Australia, and concluded that these beds are not younger than 'Lower Keuper' in age. Menendez (1951) was of the same opinion and stated that there is sufficient evidence from fossil fishes and plants to support Frenguelli's estimate of the ages of these beds. Also it must be pointed out that the 'Lower Keuper' is now considered equivalent to the Upper Ladinian, i.e. Upper Middle Triassic (see Jones and de Jersey 1947). However, the following observations indicate that the flora of the Potrerillos Beds is not younger than Middle Triassic in age.

Table 2 shows the complete list of plants known from the Potrerillos Beds of the Cacheuta Formation, and their occurrence in other Southern Hemisphere floras. No comparison has been made with contemporary floras of the Northern Hemisphere, because there are hardly any species in common. Besides the papers referred to in the text above, the following papers were consulted in preparing this table: Arber (1917), Du Toit (1932), Feistmantel (1881), Hill (1930), Lele (1955, 1962), Nye and Blake (1938), Sahni (1922, 1926), Seward (1933), and Walkom (1918, 1919, 1924, 1925 *a, b*).

It will be seen that out of the 42 listed species, 15 are confined to this flora, and hence are of not much stratigraphic value. However, many of them are represented by closely allied species in the contemporary floras. Of the remaining 27, 21 (more than 77%) occur in the flora of the Ipswich 'Series' of Queensland (mostly in the beds of Kholo and Tivoli Stages), 13 (about 48%) in the Molteno beds of the Stormberg 'Series' of South Africa, 11 (more than 40%) in the Triassic beds of Tasmania, and 9 (more than 33%) in the Esk 'Series' of Queensland. Thus the flora of the Potrerillos Beds has strong affinities, and is contemporaneous with, the floras of the Ipswich and Esk 'Series' of Queensland, Triassic of Tasmania, and Molteno beds of South Africa.

As regards the ages of the above floras, they were also previously considered to be of Upper Triassic to Rhaetic ages, but more recently they have been shown to be of Middle Triassic age (Thomas 1933; Watson, *in* Thomas 1933; Townrow 1957; Bryan and Jones 1946, 1950; Jones and de Jersey 1947; Allen 1961). Jones and de Jersey (1947) have indicated that the flora of the Ipswich 'Series' is not younger than 'Lower Keuper' (Middle Triassic), though in their correlation scheme the 'Series' has been shown to range from Lower Triassic to the basal part of the Upper Triassic. In Table 2, it is significant that out of 27 species, there are 9 in common with the flora of the Esk 'Series'. The Esk 'Series' is considered to be equivalent to the Kholo Stage of the Ipswich 'Series'.

TABLE I
Stratigraphic correlation of various Triassic strata of Argentina according to Groeber and Stipanovic 1952

Stage	Mendoza		San Juan		La Rioja		Patagonia
	South	North	Barreal	Hilario	South	North	
Rhaetian	Estratos de Llantenes	Estratos de Rio Blanco	Estratos del Rio de Los Patos Estratos de Cepeda	Estratos de Hilario	Estratos de Los Colorados or Gualo	'Cretacico superior andino'	Paso Flores and Malacara
		Estratos de Cacheuta			Estratos de Ischignu-lasto		
		Estratos de Potrerrillos	Estratos de la Cortaderita	Estratos del Alcazar	Estratos de Los Rastros		
Norian	Estratos de Chihui	Estratos de La Cabras (s.l.)	Estratos de Barreal	Estratos del Agua de Los Pajaritos	Estratos de Eschichuca		? ↑ Chacay-Co
Carnian	Upper	Choiyoiitense					Choiyoiitense and
	Middle						
	Lower						
			Palaeozoic	Palaeozoic	Palaeozoic	Palaeozoic	Palaeozoic and/or Pre-Cambrian

Kholo and Tivoli are the two oldest stages of the Ipswich 'Series' (Bryan and Jones 1950). Therefore, even if the uppermost strata of the Ipswich 'Series' belong to the basal part of the Upper Triassic, the comparison is strong with the Middle Triassic strata of the

TABLE 2

Distribution of species of the flora of Potrerillos Beds of Argentina in other floras of the Southern Hemisphere.

No.	Species	Beaufort	Molteno	New Zealand	Ipswich	Waboon	Esk	Tasmania	Narrabeen	Hawkesbury	Wianamatta	Parsora	Panchet
1.	<i>Phyllothea australis</i> Brongniart	*	—	—	*	—	—	*	*	—	*	—	—
2.	<i>Neocalanites carreri</i> (Zeiller) Halle	*	*	—	—	—	—	*	—	—	—	—	—
3.	<i>Equisetites fertilis</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
4.	<i>Sphenopteridium</i> sp. aff. <i>truncatum</i> Kurtz	—	—	—	—	—	—	—	—	—	—	—	—
5.	<i>Callipteridium argentinum</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
6.	<i>Cladophlebis kurtzi</i> Frenguelli	—	*	—	—	—	—	—	—	—	—	—	—
7.	<i>Cladophlebis mesozoica</i> Kurtz	—	—	—	*	—	—	—	—	—	—	—	—
8.	<i>Cladophlebis johnstoni</i> Walkom	—	—	—	*	—	*	*	—	—	—	—	—
9.	<i>Cladophlebis australis</i> (Morris) Seward	—	*	—	*	*	*	*	—	*	*	—	—
10.	<i>Cladophlebis copiosa</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
11.	<i>Cladophlebis wielandi</i> sp. nov.	—	—	—	*	—	—	—	—	—	—	—	—
12.	<i>Sagenopteris longicaulis</i> Du Toit	—	*	—	—	—	—	—	—	—	—	—	—
13.	<i>Thinnfeldia dutoiti</i> sp. nov.	—	*	—	—	—	—	—	—	—	—	—	—
14.	<i>Thinnfeldia praecordillariae</i> (Freng.)	—	—	—	—	—	—	—	—	—	—	—	—
15.	<i>Dicroidium odontopteroides</i> (Morris) Gothan	*	*	*	*	*	*	*	*	*	*	*	*
16.	<i>Dicroidium feistmanteli</i> (Johnston) Gothan	*	*	—	*	*	*	*	*	*	*	*	*
17.	<i>Dicroidium coriaceum</i> (Johnston) Townrow	—	*	—	*	*	*	*	*	*	*	—	—
18.	<i>Xylopteris rigida</i> (Dun) comb. nov.	—	—	—	*	*	*	—	—	—	—	—	—
19.	<i>Pteruchus rhaetica</i> (Geinitz) comb. nov.	—	*	—	—	—	—	—	—	—	—	—	—
20.	<i>Fanerotheca extans</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
21.	<i>Feruglioia samaroides</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
22.	<i>Yabeiella wielandi</i> Oishi	—	—	—	*	—	—	—	—	—	—	—	—
23.	<i>Yabeiella spatulata</i> Oishi	—	—	—	*	—	—	—	—	—	—	—	—
24.	<i>Yabeiella brackebushiana</i> (Kurtz) Oishi	—	*	—	*	—	—	—	—	—	—	—	—
25.	<i>Yabeiella crassa</i> Jones and de Jersey	—	—	—	*	—	—	—	—	—	—	—	—
26.	<i>Yabeiella mareyesiacae</i> (Geinitz) Oishi	—	—	—	*	—	*	—	—	—	—	—	—
27.	<i>Baierophyllites florinii</i> gen. et sp. nov.	—	—	—	—	—	—	—	—	—	—	—	—
28.	<i>Sphenobaiera argentiniae</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
29.	<i>Sphenobaiera tenuifolia</i> (Johnston) comb. nov.	—	*	—	*	—	—	*	—	—	—	—	—
30.	<i>Czekanowskia</i> sp.	—	—	—	*	—	—	*	—	—	—	—	—
31.	<i>Baiera cuyana</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
32.	<i>Baiera rollerii</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
33.	<i>Ginkgoites bidens</i> (Tenison-Wood) Florin	—	—	—	*	—	*	*	—	—	—	—	—
34.	<i>Ginkgoites truncata</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
35.	<i>Ginkgoidium bifidum</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
36.	<i>Phoenicopsys elongatus</i> (Morris) Seward	—	*	—	*	*	*	*	—	—	—	—	—
37.	<i>Desmiophyllum</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—
38.	<i>Stachyopitys anthoides</i> Frenguelli	—	—	—	—	—	—	—	—	—	—	—	—
39.	<i>Noeggerathiopsis</i> sp.	—	—	—	—	—	—	—	—	—	—	*	—
40.	<i>Podozamites lancolatus</i> var. <i>genuinus</i> Heer	—	—	—	—	—	—	—	—	—	—	—	—
41.	<i>Fraxinopsis major</i> Wieland	—	—	—	*	—	—	—	—	—	—	—	—
42.	<i>Fraxinopsis minor</i> Wieland	—	—	—	—	—	—	—	—	—	—	—	—
Totals		4	13	1	21	4	9	11	3	3	4	2	1

Note: In the table *(u) indicates the occurrence of the species based on an unpublished thesis reported in Jones and de Jersey (1947).

Ipswich 'Series'. The unavoidable conclusion is that the flora of the Potrerillos Beds of the Cacheuta Formation is not younger than Middle Triassic in age.

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SILURIAN LEPTAENIDS (BRACHIOPODA)

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ABSTRACT. Following the work of Poulsen (1943) the paper discusses the standing of *Leptaena rhomboidalis* (Wahlenberg 1821) and *Leptaena depressa* (James Sowerby 1825). The two species are redescribed and neotypes selected. Two new species of *Leptaena* are described: *Leptaena poulsenii* and *Leptaena arberae* from the Wenlock Limestone of England. A new genus of leptaenid brachiopods is erected and the type species, *Ludfordina pixis* sp. nov., is described. This species is from the Lower Ludlow of Shropshire, England.

THE authorship and identity of *Leptaena rhomboidalis* have been subjects of considerable uncertainty. In order to make possible the description of related forms, it was necessary to determine the nature of the species. This paper examines and supports the argument propounded by Poulsen (1943).

(a) *Leptaena rhomboidalis* (Wahlenberg 1821). The name attributed to Wilckens (1769) is invalid, since it fails to conform to the binary convention and the species must, therefore, be ascribed to Wahlenberg, as *Anomites rhomboidalis* Wahlenberg 1821. In describing his species, Wahlenberg cited figures from two authors: Wilckens 1769 and Hüpsch 1781. Wilckens's specimens were collected near Stargardt, in Pomerania, probably from Gotlandian erratics, which are not uncommon in that district (Poulsen 1943, p. 20). Hüpsch (1781) described a species from the Eifel, which may be of Devonian age.

The author has not been able satisfactorily to recognize Hüpsch's species either from description or figures and excludes it from the present restricted description, which is based upon Wilckens's figures. It is suggested that their comparison with those of Poulsen (1943) fig. 7 and with Plate 98, fig. 1 of the present paper leaves no reasonable doubt regarding the identity of the species Wilckens illustrated.

James Sowerby (1825) described a generally similar species from Dudley, England, under the name *Producta depressa* and such specimens were, until the publication of Davidson's (1871) monograph, variously described as *Producta*, *Leptaena*, or *Strophomena depressa*. Davidson regarded Sowerby's species as synonymous with *Anomites rhomboidalis* Wahlenberg, which he attributed to Wilckens, and the name *Leptaena depressa* fell into disuse. Many specimens in our older collections are, however, still so labelled.

Hisinger (1827, p. 333) published, without description, the name *Terebratula rugosa*, which remained *nomen nudum* until Dalman (1828) adopted it. The *Terebratula rhomboidalis* preceding it in Hisinger's list is not a *Leptaena* (Dalman 1827, p. 146), although it may be surmised that its presence may have influenced Dalman to adopt the trivial name *rugosa* in place of the older *rhomboidalis* in naming his species. He was, at this time, publishing his new genus *Leptaena*, under which he described, with figures, *Leptaena rugosa* and *Leptaena depressa* (Sowerby). Under each of these he gave *Anomites rhomboidalis* Wahlenberg in his synonymy, under the former as 'cum *L. depressa* commixta' and under the latter as 'cum *L. rugosa* commixta'. It may then be argued that he regarded *Leptaena rhomboidalis* (Wahlenberg) as composite and partly referable to *Leptaena*

depressa (Sowerby). By inference he referred the remainder to *L. rugosa*, a newer name which would then, in modern practice, become a junior synonym of *L. rhomboidalis* (Wahlenberg) under Article 31. King (1846) selected *L. rugosa* Dalman as the type species of *Leptaena* Dalman, but it has not frequently been used, due to doubt as to its status and identity.

Spjeldnæs (1957) rediscovered Dalman's specimens of *L. rugosa*, selected a lectotype and redescribed the species. It is clearly not conspecific with *L. rhomboidalis* (Wahlenberg) as here restricted, which is a Silurian species; *L. rugosa* Dalman is from the Ordovician.

(b) *Leptaena depressa* (James Sowerby 1825). Sowerby, in describing his *Producta depressa*, presented a composite figure (pl. 459, fig. 3) showing two exteriors, one ventral and one dorsal interior. He said: '—they are all taken from two masses of Dudley limestone, but are grouped together so as to occupy less space, and the essential parts are made rather conspicuous.' He described his species as follows: 'Nearly semi-circular, depressed, corrugated, longitudinally striated: upper portion convex near the beak, concave near the margin; front abruptly descending.'

The two upper specimens in his figure, the exteriors, are undoubtedly referable to *Leptaena*, as is probably the lower right-hand one, a dorsal interior. The lower left-hand specimen, a ventral interior, shows a denticulate hinge-line and is probably, therefore, a *Strophonella* (?*funiculata*) since the trail is ventrally directed.

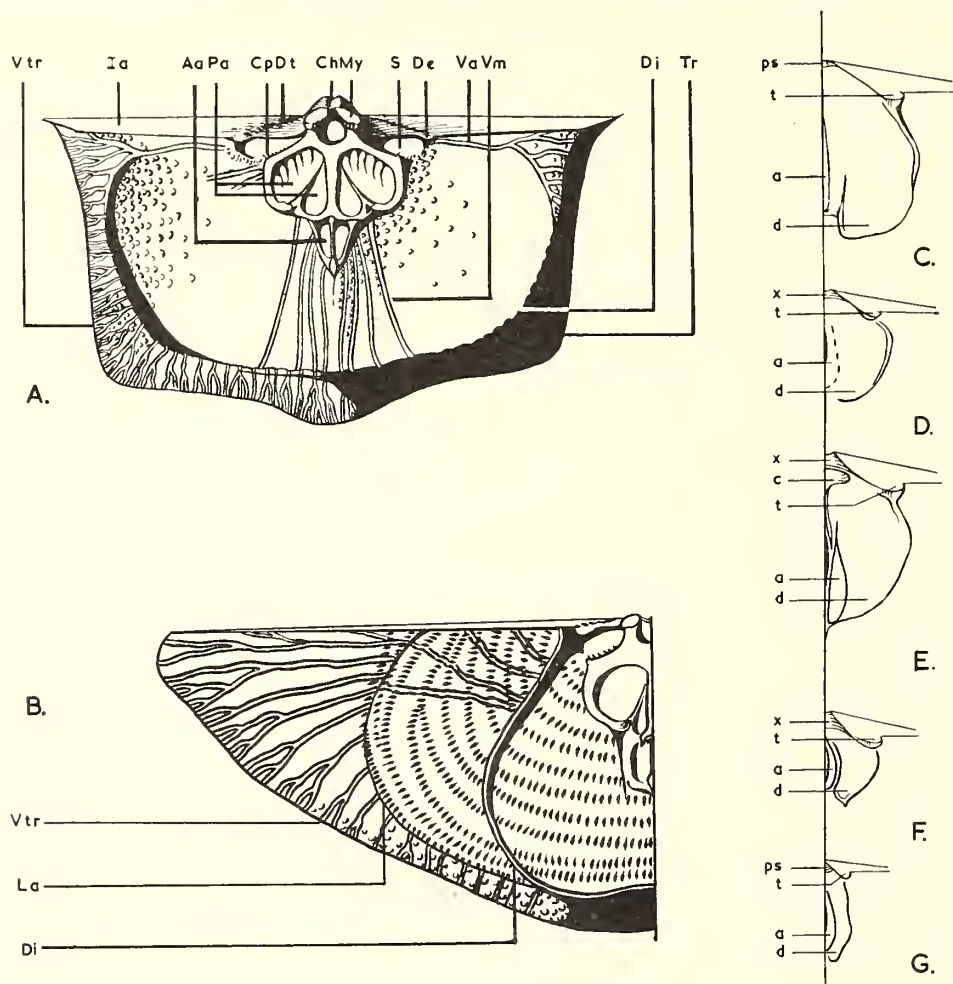
In both *Leptaena* and *Strophonella* the dorsal valve is initially concave and the ventral valve convex. Hence, Sowerby's 'upper portion convex near the beak' can only apply in these genera, to the ventral valve. 'Concave near the margin' applies to some species of *Leptaena* and all species of *Strophonella*. He then, however, says 'front abruptly descending' and, since it has been shown that he is describing a ventral valve, he can only mean that the front, i.e. the trail, is deflected dorsally. But the lower left-hand figure shows a trail unmistakably deflected ventrally and is therefore to be excluded as disagreeing with his description. The remaining figures and the description agree closely with a species of *Leptaena* common in the Dudley (Wenlock) limestone, Sowerby's type-locality. The depressed region inside the periphery of the ventral exterior is characteristic and there is general agreement in size. The original specimens figured by Sowerby are no longer to be found, but several specimens identified by him are in the possession of the British Museum (Natural History). From these a neotype has been chosen (B60949) and is figured here.

Descriptions of *Leptaena rhomboidalis* (Wahlenberg 1821) and *Leptaena depressa* (James Sowerby 1825) are offered in the present paper to amplify those of their authors and to describe their internal characters.

Terminology. Text-fig. 1 illustrates the terminology used in this paper; one new term is introduced. At the line of geniculation in *Leptaena* a ridge of secondary shell-substance is developed, which surrounds and defines the visceral disc. The ridge is here called the *apophragm* (*apo*—away, *phragm* from *phrassain*—to fence). It is usually present only in the dorsal valve, but may be developed in the ventral valve of alate species such as *Leptaena poulsenii* sp. nov.

Williams and Rowell (1965, fig. 74) have applied the term diaphragm to this structure, but by definition (*ibid.*, p. 144) this seems inapt. Diaphragm has been variously used by

Girty (1910), Muir-Wood (1928), and Ulrich and Cooper (1938). As defined by the two former authors it is, strictly, to be applied to *Productus* and *Diaphragmus*, where it is a



TEXT-FIG. 1. A. *Leptaena depressa* (J. Sowerby). Diagrammatic dorsal interior ($\times 2$); B. *Leptaena poulsenii* sp. nov. Diagrammatic dorsal interior ($\times 2$). Vtr. Vasculature on trail. Ia. Interarea. Aa. 'Anterior scars'. Pa. Adductor scars. Cp. Socket Plates. Dt. Track of denticle. Ch. Chilidium. My. Myophore. S. Socket. De. Denticle. Va. Vascula cruralia. Vm. Vascula media and myaria. Di. Apophragm. Tr. Trail. La. Lamellar wall (one young adult only); C-G Delthyrial and muscular arrangement in ventral valves of: C. *Leptaena depressa* (James Sowerby). D. *Leptaena rhomboidalis* (Wahlenberg). E. *Leptaena poulsenii* sp. nov. F. *Leptaena arberae* sp. nov. G. *Ludfordina pixis* gen. et sp. nov. ps. Pedicle callist. t. Tooth. a. Adductor scar. d. Divaricator scar. x. Pseudodeltidium. c. Pedicle collar.

thin, crescentic plate, tangential to the visceral disc, and may be costate. The apophragm in *Leptaena* is normal to the visceral disc, is unornamented, and is not crescentic in shape. As used by Ulrich and Cooper (1938) the diaphragm is exemplified in *Leptellina*,

where it is a more or less semi-circular or bilobate visceral disc, elevated above the anterior part of the valve. Williams and Rowell (1965) have redefined this as a lophophore platform.

The erection of the apophragm commences after geniculation and apparently continues throughout the life of the brachiopod. It may thus be said progressively to limit the degree of closure of the conjoint valves in response to increasing spatial requirements of the developing visceral and mantle cavities.

In describing the articulatory structure of the dorsal valve of *Leptaena* the author has preferred to follow the terminology of Spjeldnæs (1957) in using the term socket-plate, rather than that of Williams and Rowell (1965), who used the term inner socket ridge. The latter is defined as: 'Ridge of secondary shell commonly overhanging dental socket and forming its inner or anterior margin.'

In *Leptaena* the socket is formed by an elongate plate originating beneath the chilidium. The plate is concave in transverse section and forms both the floor of the socket and its inner margin. It is crenulated and is supported by lateral ridges from the notothyrial platform which form the posterior boundaries of the muscle scars.

Dorsal muscle scars in Leptaena. The central part of the mature dorsal valve of *Leptaena* bears a quadripartite impression symmetrically divided by the median septum, thus forming a pair of posterior and a pair of anterior scars. The posterior scars are sub-circular in outline and in well-preserved specimens are themselves seen to be bilobate. The anterior scars are almost triangular and terminate about the end of the median septum, which is here elevated to a delicate point. They are laterally bounded by a varying system of parallel and converging ridges. The bilobation of the posterior scars indicates that they consist of a pair of postero-lateral and a pair of antero-mesial adductor scars. The function of the anterior scars is not, however, clear.

The anterior scars resemble muscle scars, but their development as, for example, in *L. depressa*, makes such a function improbable. In the young adult shell the posterior boundary of the adductors is defined by an anchor-shaped ridge immediately in front of the cardinalia, whilst the anterior extension of the scars is concealed by the internal repetition of the external rugae and costellae. The median septum is indicated by the slightly greater development of one costella, whilst two lateral costellae are discernibly emphasized and later become the lateral bounds of the anterior scars. The mature dorsal shell shows these scars as a pair of depressions in a platform of secondary shell. The platform necessarily narrows as its height increases and in gerontic valves the depressions are filled, leaving only the crest of the median septum visible, whilst the platform falls abruptly away to the anterior floor of the valve. This may suggest the atrophy of some function at present unknown. The elevation of these scars into a platform must imply folding of the dorsal outer epithelium, which would have the effect of dividing the mantle cavity into two parts. In the ventral valve there is frequently selective deposition of shell material antero-laterally to the divaricator scars and indicating the presence of dorsally directed spirolophes. It is inferred from the position of these that the anterior body-wall and the mouth were located over the anterior scars.

Mature and gerontic specimens of *L. depressa* and *L. poulseni* are shown, Plate 98, figs. 7, 11, 12, and 9.

Vasculature in Leptaena. The majority of specimens examined for the purpose of the paper showed little indication of the origin and course of the main vasculature. Traces of the *vascula media* and *vascula myaria* are not uncommon. Occasionally the *vascula cruralia* are detectable and appear to curve forward from the lateral parts of the hinge-line, thus suggesting the commencement of the arcuate form necessary to the accepted saccate pattern. Complete *vascula arcuata* have not, however, been seen. The figured dorsal valve of *L. depressa*, Plate 98, fig. 7 shows a number of *vascula* originating immediately anterior to the sockets and from the postero-lateral adductor scars whence they partially cross the disc. Specimens of *L. poulsenii* suggest that these *vascula genitalia* may reach the apophragm. In *L. arberae* the *vascula myaria*, when seen, appear to reach and surmount the apophragm and no suggestion of *vascula arcuata* has been observed.

From this composite and somewhat tentative evidence it seems probable that the dorsal valve in *Leptaena* departs from the accepted saccate pattern and may in fact be lemniscate.

The figured dorsal valve of *L. poulsenii*, Plate 98, fig. 12, has an almost complete lateral trail which carries good impressions of the *vascula terminalia*. These have reached a stage when they may reasonably be equated with the external costellation.

Specimens numbered BU are deposited in the Department of Geology, Birmingham University; those labelled BMNH are in the British Museum (Natural History).

SYSTEMATIC DESCRIPTIONS

Superfamily STROPHOMENACEA King 1846

Family LEPTAENIDAE Hall and Clarke 1894

Genus LEPTAENA Dalman 1828

Leptaena rhomboidalis (Wahlenberg 1821)

Plate 98, figs. 1-3

- 1821 *Anomites rhomboidalis* Wahlenberg, p. 65.
- non 1828 *Leptaena rugosa* Dalman, p. 106, fig. 1.
- non 1871 *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, figs. 1-21.
- 1943 *Leptaena rhomboidalis* (Wilckens); Poulsen, pp. 19-21, fig. 7a-d.
- non 1965 *Leptaena rhomboidalis* (Wilckens); Williams and Rowell, fig. 252, 5d-e.

Diagnosis. Semi-oval to rhomboid, with fine radial costellae and very deeply incised rugae. Foramen large, truncating the pseudodeltidium which covers the entire delthyrium. Ventral muscle scar sub-pentagonal; adductors poorly defined, not enclosed by diductors.

Neotype. Here selected, BU 878. *Paratypes.* BU 879, BU880.

Locality and horizon. Upper Visby Marl, Visby, Gotland. I am informed by Professor Regnéll, now of Lund, that there is frequently some doubt regarding the provenance of many specimens bearing the name *L. rhomboidalis*, the locality Visby often being synonymous with Gotland. The possible horizons seem to be Upper Valentian-Lower Wenlock, i.e. Upper Visby Marl or Hogklint group. The species is thus from horizons lower than those providing the British species described below, which are from the Wenlock Limestone and lower Ludlow.

Description. Disc transversely semi-oval to rhomboid, its greatest width, a little anterior to the hinge-line, about 24 mm., but may reach 37 mm. in old specimens. Trail geniculated more or less abruptly, curving dorsally, laterally produced into ears. Trail forms half the total length, which is 24–27 mm.

Radial ornament of fine costellae, increasing by intercalation and bifurcation. Concentric rugae 8–12, deeply incised and widely spaced. Foramen penetrates the beak, truncating the pseudodeltidium which covers the delthyrium. Chilidium high, grooved. Contour of ventral valve convex about the beak, becoming flatter towards the edge of the disc. Contour of dorsal valve follows generally that of the ventral and is gently concave.

Dorsal interior. Apophragm outlines an almost completely oval disc, truncated towards the middle of the hinge-line, and is relatively low and sharp crested. Cardinal process bifid, myophores narrow and slender, shafts slightly diverging. Socket-plates small, crenulated; opposite each one is a denticle, carried on the edge of the interarea. Adductor scars sub-circular, faintly bilobate, bounded by ridges produced from the notothyrial platform. Anterior scars not strongly defined, about half the width of the adductor scars. Median septum extending to two-thirds of the length of the disc, dividing anterior scars which are laterally bounded by fine ridges.

Ventral interior. Diductor scars sub-pentagonal, bounded by a strong ridge; adductor scars poorly defined, not enclosed by diductors. Teeth small, supported by receding dental lamellae.

Comparisons. This species is most easily recognized by its strongly rugose exterior, which no other species has so well-developed. In radial ornament it is nearly approached by *L. poulsenii* sp. nov., which has a similar development of foramen and pseudodeltidium. The latter species is, however, so strongly alate that no confusion of entire specimens is possible. As in all the species here described, the ventral muscle scars are distinguishing features. They are shown in text-fig. 1 c–g. *L. rhomboidalis* (Wahlenberg) is usually slightly larger than *L. arberae* sp. nov. which also has a similar foramen and pseudodeltidium; the latter is less rugose and its radial ornament is not thread-like.

Leptaena depressa (James Sowerby 1825)

Plate 98, figs. 4–9

1825 *Producta depressa* James Sowerby, p. 86, pl. 459, fig. 3.

1871 *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, figs. 3, 5, 12, 14 only.

Diagnosis. Semi-circular to quadrate or rhomboid, having radial costellae with small interspaces and rugae not coarsely developed. Foramen small, often cicatrized; pseudodeltidium small covering only umbonal part of delthyrium. Ventral valve depressed immediately inside line of geniculation. Ventral muscle scar large, widely cordate. Adductors anteriorly elevated, shorter than diductors.

Neotype. Here selected, BMNH B60649. *Paratypes.* BU 882, BU 881, BMNH B43364.

Locality and horizon. Wenlock Limestone, Dudley, England.

Description. Outline semi-circular to quadrate or rhomboid, widest at the hinge-line, about 40 mm. Total length approximately equal to the width, trail forming half the length. Small acute ears developed at the cardinal extremities, from which the trail is abruptly geniculated all round. Rugae relatively fine, 13–18 in number; radial costellae closely spaced. Ventral valve convex about the beak but typically depressed immediately before the line of geniculation. A small foramen may be present but is usually sealed internally or cicatrized. Pseudodeltidium small, chilidium high.

Dorsal interior. Disc outlined by a strong apophragm, highest anteriorly, curving inwards posteriorly to the hinge-line. Cardinal process bifid, myophores and shafts sub-parallel in young adults, but divergent in gerontic specimens. Socket-plates crenulated. Outer wall of each socket formed by inner edge of interarea from which a denticle is produced.

Adductor scars bilobate, outlined by sub-circular ridges from the notothyrial platform. Median septum extends for about three-quarters of the length of the disc, where it is pointed and where the anterior scars terminate. Latter about one third as wide as the adductor scars, bounded by lateral ridges meeting at an acute angle at the termination of the median septum.

Ventral interior. Muscle scar cordate, diductors wide. Adductor scars elevated, shorter than the diductors, which do not enclose them. Teeth strong, crenulated except in old specimens and supported by dental lamellae which are produced forwards and are continuous with the ridges outlining the muscle scars. A transverse plate is present in the apex of the delthyrial cavity. A low ridge is developed round the inside face of the trail, marking the line of contact of the articulated valves. On specimens having a quadrate or rhomboid outline the trail frequently shows three lobes.

EXPLANATION OF PLATE 98

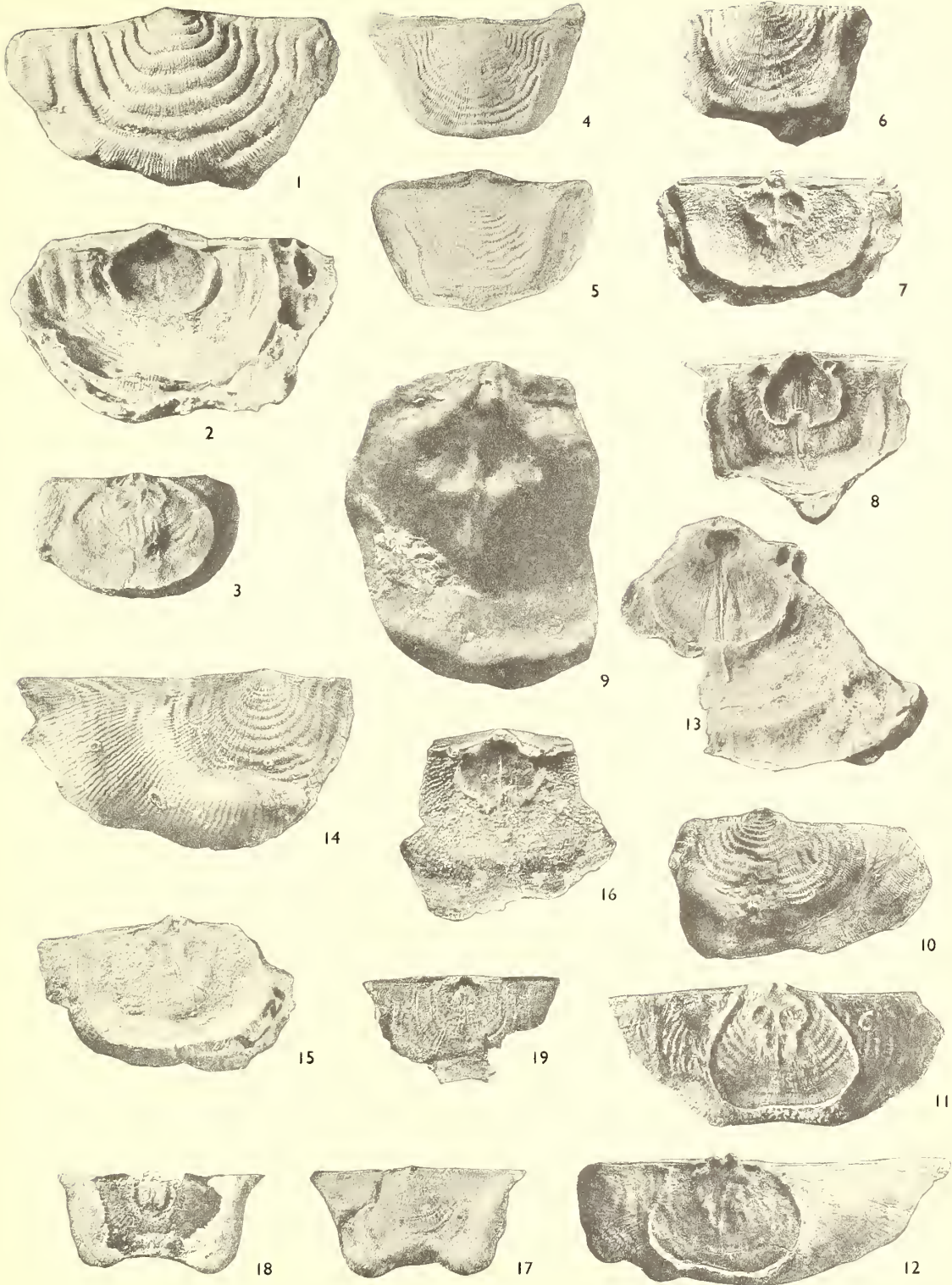
Figs. 1–3. *Leptaena rhomboidalis* (Wahlenberg). Upper Visby Marl or Hogklint Group, Gotland. 1, Ventral exterior of neotype ($\times 2$), BU 878. 2, Interior of ventral valve ($\times 2$), BU 880. Incompletely cleaned due to crystallization in the floor of the valve. 3, Interior of a large dorsal valve ($\times 1$), BU 879.

Figs. 4–9. *Leptaena depressa* (James Sowerby). 4, 5, Ventral and dorsal exteriors of neotype ($\times 1$), BMNH B60949. Wenlock Limestone, Dudley, England. 6, Ventral exterior of topotype ($\times 1$), BU 881. Wenlock Limestone, The Wren's Nest, Dudley, England. 7, Dorsal interior of topotype ($\times 1$), BU 882. Locality and horizon as fig. 6. 8, Ventral interior, showing trilobation of trail. Topotype ($\times 1$), BMNH B43364. Wenlock Limestone, Dudley, England. 9, Part of dorsal interior, showing gerontic development of scars ($\times 2$), BU 877. Locality and horizon as fig. 6.

Figs. 10–13. *Leptaena poulsenii* sp. nov. 10, Ventral exterior of an almost complete specimen. The interrupted hinge-line and irregular rugae show that the specimen suffered injury from which it recovered ($\times 1$), BU 890. Wenlock Limestone, The Wren's Nest, Dudley, England. 11, Dorsal interior of young adult ($\times 1$), BMNH B43361. Wenlock Limestone, Dudley, England. 12, Dorsal interior of holotype ($\times 1$), BU 889. Wenlock Limestone, The Wren's Nest, Dudley, England. 13, Fragmentary ventral interior showing pedicle collar ($\times 2$), BU 891. Locality and horizon as fig. 12.

Figs. 14–16. *Leptaena arberae* sp. nov. 14, Ventral exterior of holotype ($\times 2$), BU 887. Locality and horizon as fig. 12. 15, Dorsal interior ($\times 2$), BU 886. Locality and horizon as fig. 12. 16, Ventral interior ($\times 2$), BU 888. Locality and horizon as fig. 12.

Figs. 17–19. *Ludfordina paxis* gen. et sp. nov. Lower Ludlow Mudstones, Upper Millichope, Shropshire, England. 17, Ventral exterior of holotype ($\times 2$), BU 883. 18, Ventral interior (mould) ($\times 2$), BU 884. 19, Dorsal interior (mould) ($\times 2$), BU 885.



KELLY, Silurian *Leptaena*

Comparisons. *L. depressa* differs from the other species described here in the poor development of the foramen and pseudodeltidium. In radial ornament it is most closely approached by *L. arberae* sp. nov. which is, however, much smaller and has a large pseudodeltidium and an open foramen. *L. 'rhomboidalis'* var. *eta* Reed (1917, pl. 13, figs. 5–7) shows a depression of the ventral exterior inside the line of geniculation. The latter lacks the abrupt geniculation of *L. depressa* and seems never to develop the quadrate or rhomboid shape common in the latter. The ventral musculature of *L. depressa* is most closely approached by *L. 'rhomboidalis'* var. *gamma* Reed (1917, pl. 12, figs. 2–3), but the latter is more strongly rugose. *L. rugosa* Dalman differs in its flabellate ventral muscle scar and greatly depressed region of the ventral exterior.

Discussion. *L. depressa* is the commonest of the species of *Leptaena* found at Dudley, although in some exposures it may be outnumbered by *L. poulsoni* sp. nov. or *L. arberae* sp. nov. The species, or its varieties, extends throughout the Wenlock and into the Leintwardinian. The above description is applied to specimens from the horizon and locality specified, since Sowerby's specimens were collected from these beds.

A single specimen examined, BU 892, shows slightly aberrant articulation in that it has developed a series of minor denticles between the antero-lateral edge of the chilidium and the normal denticle developed at the lateral edge of the socket. Professor Spjeldnæs informs the writer (*in lit.*) that he has found such a development not uncommon in gerontic valves. Since, however, this specimen shows a growth-track preceding each of the minor denticles, they must clearly have been present at all stages of growth. Reed (1917, p. 873) claimed to have seen minute denticles along the entire hinge-line in *L. zeta* Lamont 1947. The writer has not observed this in any of the species described in the present paper.

Leptaena poulsoni sp. nov.

Plate 98, figs. 10–13

1871 *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, figs. 1, 10, 11, 15 only.

Diagnosis. Transversely semi-oval in outline, having highly alate lateral extensions. Ornament of thread-like radial costellae and coarse concentric rugae. Foramen large, open, pseudodeltidium large, covering the entire delthyrium. Ventral muscle scar sub-circular, adductors and diductors of equal length.

Holotype. BU 889. *Paratypes.* BU 890, BU 891, BMNH B43361.

Locality and horizon. Wenlock Limestone, The Wren's Nest, Dudley, England.

Description. Outline transversely semi-oval, about 70 mm. wide at the hinge-line, the widest part of the shell, and about 40 mm. long at the median line, the trail forming about half the total length. Trail curved in front, geniculated through a right angle at the middle, angle of geniculation decreasing to zero at the cardinal angles. The disc forms the middle portion of the shell, about 30 mm. wide, 20 mm. long. Rugae number 13–18, extending on to the ears. Outer rugae directed towards the cardinal angles, those nearer the beak converging or intersecting the hinge-line at a right angle. Costellae fine, interspaces relatively wide with closely spaced growth-lines. Costellae increase by

intercalation. Foramen large, truncating the pseudodeltidium. The latter covers the entire delthyrium.

Ventral valve convex about the beak, flattening out laterally and towards the front. Dorsal valve concave.

Dorsal interior. Disc outlined by a thin, relatively high apophragm; widest towards the front, in shape oval to scutiform. Myophores and shafts of the cardinal process sub-parallel to divergent. Socket-plates crenulated. Posterior edge of socket formed by interarea, carrying a denticle opposite each socket-plate.

Adductor scars sub-circular, bilobate, outlined by ridges from the notothyrial platform. Low median septum extending a little over half the length of the disc, where it is pointed, defining the anterior extension of the anterior scars. The latter defined laterally by ridges from which offshoots converge at the termination of the septum. Anterior scars about half as wide as the adductor scars.

Ventral interior. Ventral disc similar in shape to dorsal, laterally defined by an apophragm. Teeth strong, supported by lamellae which continue forward with the ridges bounding the diductor scars. In older specimens secondary shell unites the pseudodeltidium, dental lamellae, and the floor of the valve, forming a pedicle-collar with the foramen at its apex. Diductors semicircular, a low median ridge carrying the adductor scars. Both pairs of muscles are of equal length. Inner face of teeth crenulated, except in old specimens.

Comparisons. In ornament, rugosity, and deltidial development *L. poulseni* resembles *L. rhomboidalis* with which it is compared above. It is differentiated from others described here by its extreme alation and its ventral musculature. A similar form from the early Devonian (Birdson Shales, Tennessee) of the United States is figured by Cooper (1944, pl. 132, fig. 16) as *L. rhomboidalis*. The American species appears to be closely related to *L. poulseni*.

Discussion. *Leptaena poulseni* was figured by Davidson (1871), with other species, as *L. rhomboidalis*. Plate 39, fig. 15 was incorrect in that it showed a ventral interior of *L. poulseni* having the muscle scars of *L. depressa*, i.e. having adductors shorter than diductors. The specimen is BMNH B8340 and has adductors and diductors of equal length. The pedicle-collar developed in the specimen figured in this paper is not, however, present in Davidson's specimen. His figure shows the ventral apophragm correctly.

Leptaena arberae sp. nov.

Plate 98, figs. 14-16

Diagnosis. Small *Leptaena* of sub-quadrate to ovate outline having a variable degree of alation, rugose, costellate. Foramen open, pseudodeltidium well-developed, covering the entire delthyrium. Ventral adductors shorter than diductors, scar semicircular.

Holotype. BU 397. *Paratypes.* BU 396, BU 398.

Locality and horizon. Wenlock Limestone, The Wren's Nest, Dudley, England.

Description. Disc sub-quadrate to ovate; ears small and acute in young specimens, well developed in older ones. Shell widest at the hinge-line, 25-40 mm. according to age.

Length of disc at median line about 10 mm. and the total length, including the trail, about 18 mm. Shell geniculated through 90° and at the median point of geniculation a slight lobation may be discernible, not extending to the trail. Foramen, chilidium, and pseudodeltidium well developed. Radial costellae closely spaced, increasing by bifurcation and intercalation. Immediately preceding bifurcation they tend to thicken and become flattened. Rugae never coarsely developed, becoming progressively finer from the line of geniculation to the beak. Outer ones diverging sharply towards hinge-line, inner ones parallel or tending to converge.

Dorsal interior. Disc transversely oval, defined by strong apophragm and truncated posteriorly by the hinge-line. The apophragm often shows a slight ventrally directed lobe at the middle line. Myophores and shafts of cardinal process sub-parallel. Socket-plates crenulated, posterior edge of socket formed by interarea and carrying a denticle opposite each socket-plate. Adductor scars defined by sub-circular ridges. Low median septum extends to about three-quarters of the length of the disc. Anterior scars triangular and pustulate. Young specimens show them bounded by thin, parallel or divergent ridges.

Ventral interior. Teeth fairly robust, crenulated, supported by receding dental lamellae. Adductor scars not prominent, separated by a thin ridge. Diductors, the longer of the two sets of scars, bounded laterally by curved ridges which give a pointed outline to each scar at its anterior extremity.

Comparisons. *L. arberae* is distinguished from *L. depressa* and from *L. poulsenii* by its smaller size and thicker costellae. The interspaces between costellae are much reduced and the costellae themselves tend to flatten and become thicker preceding bifurcation. The ventral muscle scars are broadly semi-circular, as in *L. poulsenii*, but the anterior production of each diductor scar into a point and the recession of the dental lamellae in *L. arberae* distinguish the two species. The dental lamellae, however, resemble those of *L. rhomboidalis*, which it also approaches in size and foraminal development. Their external ornament is, however, different and they appear at different horizons.

Genus LUDFORDINA gen. nov.

Type species. *Ludfordina paxis* sp. nov.

Diagnosis. Small leptaenid brachiopods having a more or less pronounced antero-median sulcus. Both valves sharply geniculate dorsally; radial ornament and rugae obsolescent. Ventral muscle-scars elongate, dorsal ones not strongly defined.

Range. As presently known the genus ranges from the Middle Ordovician (Norway) to the Ludlovian (England).

Discussion. *Ludfordina* embraces two species, *Ludfordina paxis* sp. nov. from the Ludlovian and *Leptaena minuta* Kiaer from the Middle Ordovician. Its erection is justified by the consistency of its diagnostic features as exemplified in these two species. Spjeldnæs (1957, p. 213) suspected that *Leptaena minuta* Kiaer might be placed in *Cyphomena* Cooper. The latter genus, however, is non-rugose on the disc, not sharply geniculate, and its ventral musculature is wider relative to its length. *Notoleptaena* Gill and

Rugoleptaena Havlíček are similar to the new genus, but are ventrally geniculate whilst having a dorsally directed median trail.

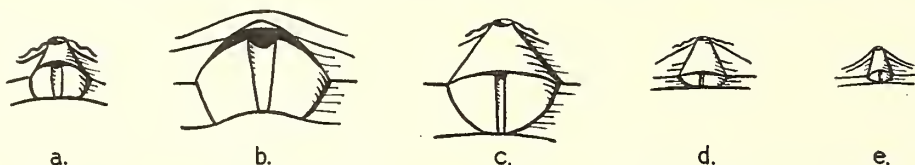
Ludfordina pixis sp. nov.

Plate 98, figs. 17-19

Holotype. BU 883. *Paratypes*. BU 884, BU 885.

Locality and horizon. Upper Millichope, Shropshire, England. Stream section in Lower Ludlow mud-stones.

Description. Outline rhomboid, hinge-line forming widest part of the shell. Small acute ears developed at cardinal extremities from which the lateral margins converge and curve inwards towards the front. At the line of geniculation there is a well-marked median



TEXT-FIG. 2. Diagrammatic illustration of pseudodeltidia and chilidia in: *a*, *Leptaena rhomboidalis* (Wahlenberg); *b*, *Leptaena depressa* (J. Sowerby); *c*, *Leptaena poulsenii* sp. nov.; *d*, *Leptaena arberae* sp. nov.; *e*, *Ludfordina pixis* gen. et sp. nov. (All are to approximately the same scale.)

sulcus, characteristic of the genus. Trail sharply geniculated dorsally, about a quarter of the total length. Width at hinge-line of the holotype 15.5 mm., length at the median line 6.5 mm., lateral to the sulcus 8 mm., the depth of the sulcus is therefore 1.5 mm., but is greater in some other specimens.

From the cardinal angles a peripheral ridge follows outline of shell, increasing in height as it approaches the lobes which result from the sulcate outline. Ridge highest at these points, between them almost or entirely disappearing. Ventral valve is thus sulcate in both horizontal and vertical planes. Ventral valve convex in a narrow elongate zone about the beak, flattened and depressed towards antero-lateral margin inside peripheral ridge. Foramen and pseudodeltidium small, chilidium moderately developed. Contour of dorsal valve follows that of ventral. Ornament of poorly defined costellae and obsolescent rugae.

Dorsal interior. Components of cardinal process slender, closely set. Adductor scars faintly impressed, outlined by lateral ridges from notothyrial platform, divided by low median ridge. Latter extends as thin median septum to about two-thirds of the length of disc. Anterior scars ill-defined. Socket plates small; apophragm low, bilobate.

Ventral interior. Muscle scars relatively small, elongate, adductors occupying about one-quarter of total width, shorter than diductors and not enclosed by them. Diductors bounded by sharp sub-parallel ridges discontinuous with dental lamellae. Ridges curve inwards at anterior end, giving hook-shaped impression in casts. Low median ridge divides muscle scar in young adults, disappearing in old specimens. Teeth strong. In old specimens, beak contains a callist, longitudinally grooved.

Comparisons. *Ludfordina pixis* is distinguished by its sulcate anterior margin. In outline it therefore resembles *Rugoleptaena* [*Leptaena*] *emarginata* (Barrande), which is, however, recognized by the reversed deflection of its trail. *Ludfordina pixis* most closely resembles *Leptaena minuta* Kiaer, here included in the new genus, which is, however, smaller, and has converging ridges bounding the ventral diductors.

Discussion. Spjeldnæs (1957), in describing *Ludfordina* [*Leptaena*] *minuta*, from the Upper Cyclocrinus Beds (Middle Ordovician, Norway), states that the species is known only from the type locality (Tonerudodden) where it occurs abundantly. The writer has found *Ludfordina pixis* only at Upper Millichope, Shropshire, where it is locally abundant.

The species appears to be indistinguishable from a specimen in the Manchester Museum, examined by courtesy of Dr. R. M. C. Eager. This specimen is labelled '*Strophomena pixis* Salter ms.' and is stated to be from the Wenlock Shales, Malvern Tunnel. It is preserved in a black shaley matrix in association with *Dicoelosia* [*Bilobites*] *biloba* (Linn.). Presumably the trivial name '*pixis*' is derived from the pitch-like appearance of the matrix. The writer has been unsuccessful in finding any description published by Salter which might define the species and it seems that the name has no validity. From respect to Salter, however, the name is retained here, although not aptly descriptive for the Upper Millichope specimens, which are preserved in olive-grey mudstone.

Should later investigation reveal that the Wenlock Shale form is not conspecific with *Ludfordina pixis* then a new name will be required for Salter's specimen.

Acknowledgements. I wish to record my gratitude to Professor Chr. Poulsen, University of Copenhagen, for the gift of specimens and to Professor G. Regnéll, formerly of the Naturhist. Riksmuseum, Stockholm, for the loan of material. Professor L. J. Wills and Professor H. B. Whittington, lately of the University of Birmingham, loaned specimens from the collections in the Department of Geology and gave other considerable assistance. Specimens from the British Museum (Natural History) were loaned by Dr. H. M. Muir-Wood and access to Sowerby's material was granted by Dr. H. Brunton and Dr. L. R. M. Cocks, all of whom I thank. Mr. A. Ludford, Luton College of Technology, has given both aid and stimulation.

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FINE STRUCTURE OF THE EYE IN TWO SPECIES OF *PHACOPS* (TRILOBITA)

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ABSTRACT. The anatomy of the schizochroal eyes of *Phacops fecundus* Barrande and *P. latifrons* (Bronn) was investigated by sectioning. Intralensar structures were best preserved in *P. latifrons*, where each lens has an outer crescentic region, perhaps bipartite, surrounding a smaller 'proximal nucleus'. In *P. fecundus* lens structure was less distinct, but a sublensar structure was seen projecting into the central lumen of the eye and forming a long slightly tapering cylinder continuous with the corneal-intrascleral membrane. This may be analogous with the crystalline cone in recent arthropods.

In both species the sclera is thicker than the lenses, and each lens lies at the top of a cylindrical alveolus excavated in the sclera. The directions of these alveoli have been used in determining the probable original internal arrangement of the sublensar visual units. In horizontal section these are obliquely radial, in vertical section they are almost parallel and thus are not generally coaxial with the outwardly directed lens-axes. The functional significance of the latter phenomenon is obscure but may relate to day and night vision. The postulated internal arrangement necessitates shorter central visual units and longer outer ones. This would explain the observed size differentiation of the lenses on the visual surface.

THE schizochroal eyes of phacopid trilobites are distinguished from other trilobite eyes by having large biconvex lenses, separated from each other by an opaque interlensar sclera. These lenses, which rarely number above 500 per eye, and are generally much fewer, are arranged upon a visual surface approximating a lunate segment of a cone. The upper surface of each lens has a thin pellucid corneal covering, which continues at the lens margin to plunge below the surface of the interlensar sclera as a cylindrical ring free of contact with the lens.

The anatomical details were originally worked out by Lindström (1901), whose excellent figures of various structures in thin section have often been reproduced and commented upon (Hanström, 1926; Harrington *in* Moore, 1959). Lindström, however, only studied five phacopid species, and his illustrations showed just a few lenses and not sections through the whole eye. Some details of the anatomy of the eyes of three other phacopid species are known from the work of Clarke (1889), Exner (1891), and Rome (1936).

The eyes of several species of phacopids have now been sectioned as part of a research project on trilobite vision, in the hope of revealing further anatomical details, and in order to determine more about the structural and functional relationships of the various parts of the eye. In this paper the eyes of a well-preserved specimen of *Phacops fecundus* Barrande are described (no. 20575) (Silurian, Bohemia), and three specimens of *Phacops latifrons* (Bronn) (nos. 20576, 20584, and 20607) from the Devonian of North Germany, which were kindly donated for study by Miss H. C. Nisbet, Curator of the Grant Institute of Geology. In each of these, only a single eye-variant was studied. Lens-distribution diagrams are given (text-figs. 1*b*, 2*e*) for comparison with existing work (Clarkson, 1966*c*).

Methods of study. In order to reduce danger of disintegration during preparation, the specimens were embedded prior to grinding in blocks of clear 'Araldite', and the surfaces of these blocks were polished so

that the eyes could be clearly seen. Where specimens possessed two intact eyes the blocks were halved; one eye being used for vertical and the other for horizontal sectioning.

Horizontal sections were made by grinding the blocks parallel with the horizontal rows of lenses (for terminology see Clarkson 1966*a*). At each level when important structural detail was visible the cut face was polished with fine carborundum powder, etched for a few seconds in dilute hydrochloric acid, and then examined in reflected light using immersion oil under a coverslip. Colour changes limiting organic junctions were clearly seen by this method; they were more easily visible than in thin sections prepared as for petrography. Cellulose peels were taken as permanent records of all the sections cut prior to further grinding.

Each horizontal section was made, as far as possible, to include the full length of a single horizontal row, but because of the progressive downward widening of the spaces between dorso-ventral files these horizontal rows are not entirely planar; the central lenses lie at a lower level than the peripheral ones. In such sections the full separation between lenses of alternate files in a single horizontal row is visible only in the central parts of the eye, whereas peripherally parts of lenses belonging to adjacent horizontal rows are interposed (text-figs. 1*b*, 2*e*).

Vertical sections were usually cut exactly through the centres of the lenses of single dorso-ventral files so as to show the full height of the eye. They were made normal to the visual surface.

Phacops fecundus Barrande

Text-fig. 1 *a-i*, Plate 99, figs. 1-3

The external morphology and variation in the eyes of this species was well described by Barrande (1852, p. 514), and certain functional aspects were discussed by the author (Clarkson 1966*c*, pp. 471-2). Exner (1891) figured a few lenses in thin section but was unable to distinguish any intralensar or sublensar structures.

Specimen no. 20575 was well preserved though the palpebral lobes and some of the upper lenses of both eyes were damaged. There were 18 dorso-ventral files with a maximum of 6 lenses per file and the largest lenses were of diameter 0.5 mm. The original lens distribution in files from anterior to posterior was as follows:

345 656 565 555 454 432: Total 82 (text-fig. 1*b*).

Horizontal sections were made from the left eye, vertical ones from the right one.

1. Structures seen in horizontal section

Details of the lenses, cornea, interlensar sclera, and for the first time, a sublensar structure, are visible in the single section figured here (text-fig. 1*a*).

Each lens is set at the summit of a cylindrical cavity, or sublensar alveolus, excavated in the sclera (text-fig. 1*i*). The thick lenses are unequally biconvex; their inner surfaces have the higher radius of curvature. A narrow flange at the edge of each lens interlocks with a corresponding indentation just below the surface of the interlensar sclera. The

EXPLANATION OF PLATE 99

Figs. 1-3. *Phacops fecundus* Barrande. Silurian, Bohemia. Grant Institute no. 20575. 1, Left eye, sectioned horizontally as in text-fig. 1 *a, b*, showing a 'cone' below the cut lens in dorso-ventral file 14, $\times 10$. 2, Right eye, sectioned vertically through file 14, as in text-fig. 1*h*, $\times 30$. 3, Posterior region of left eye, showing the cone, as in text-fig. 1*c*, $\times 30$.

Figs. 4-7. *Phacops latifrons* (Bronn). Devonian, N. Germany. 4, Left eye of Grant Institute no. 20607, sectioned horizontally as in text-fig. 2 *a, e*, $\times 15$. 5, Left eye of specimen 20584, sectioned vertically through file 5, showing intralensar structures as in text-fig. 2 *d, g*, $\times 25$. 6, Posterior region of left eye of specimen 20607, showing intralensar structures as in text-fig. 2 *a, f*, $\times 25$. 7, Right eye of specimen 20584, sectioned vertically through file 5, as in text-fig. 2*c*, $\times 25$.



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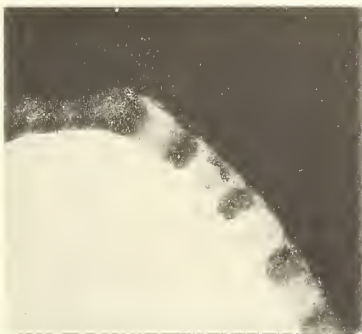
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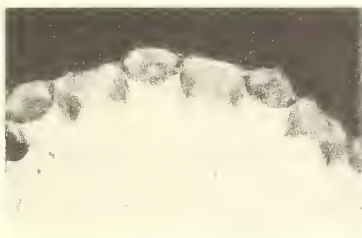
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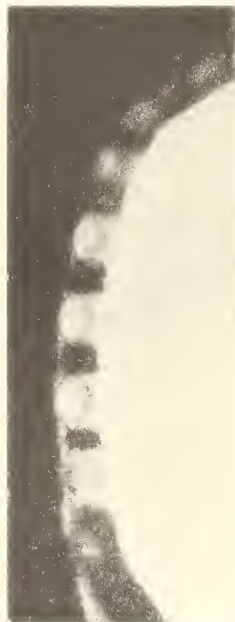
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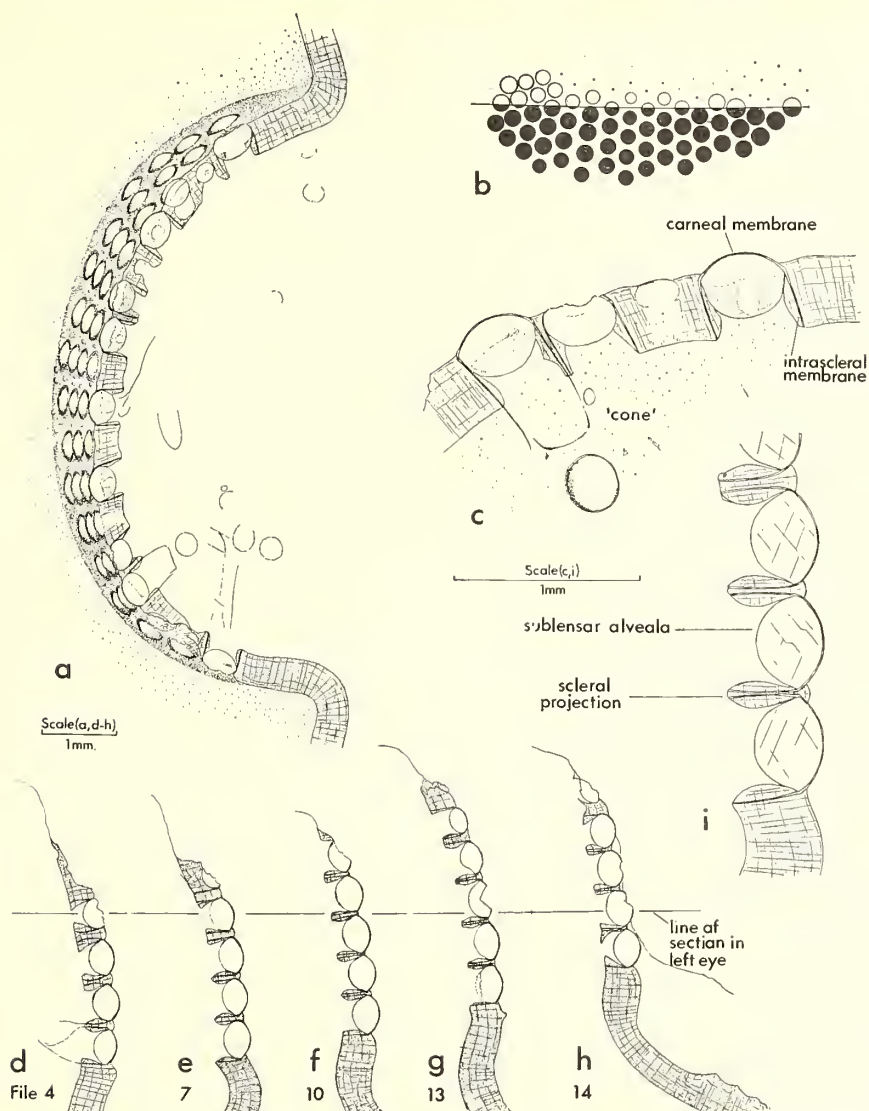
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TEXT-FIG. 1. Anatomy of the eye of *Phacops fecundus* Barrande, Grant Institute no. 20575. *a*, Horizontal section through left eye along the line shown in fig. *b*. A 'cone' is visible under the sectioned lens of the 14th dorso-ventral file. Some of the other internal structures are fragmentary cones but most are organic debris. $\times 10$. *b*, Projected visual surface of left eye, showing the line of the section fig. *a*. The blank circles represent lenses, originally present, which have been removed during preparation, the dots indicate the probable centres of lenses damaged prior to preparation. $\times 5$. *c*, Enlargement of part of the above horizontal section showing the 'cone' in the 14th dorso-ventral file, and the continuous corneal-intrascleral membrane. Traces of intralensar structure are visible. The ring below the cone is an extraneous organic fragment, possibly of algal origin and is not part of the eye. $\times 25$. *d-h*, Vertical sections through the centres of numbered dorso-ventral files. File 10 has not been cut quite normal to the visual surface. Sublensar structures in file 4 seem to represent a collapsed cone. These sections are aligned for reference according to the line of the horizontal section in the other eye. $\times 10$. *i*, Enlargement of part of file 7. The lenses of this eye have undergone recrystallization, obliterating the internal structures, and showing traces of calcite cleavage planes. $\times 25$.

outer surfaces of the lenses are always regularly curved, but their inner surfaces are not always so, for in parts of the eye where the visual surface is most strongly curved, there may be some discrepancy between the axial bearing of the outer part of the lens and the direction of the sublensar alveolus, and in such cases the inner surface is drawn out into a slight bulge in the direction of the alveolus. It may be assumed here that the sublensar ommatidium was coaxial with the alveolus, and thus that light incident on the lens in the direction of its axis would be refracted towards the photoreceptors in a slightly different direction.

Not a great deal of internal structure is visible in the lenses. They consist of microcrystalline calcite, which might indicate an element of calcite in their original constitution. Some of the lenses sectioned horizontally show a banded structure. A few have a central capsule or nucleus located near the proximal edge of the lens. Similar, but better-preserved structures were observed in the eye of *P. latifrons*.

The upper surface of each lens has a disjunct corneal membrane which plunges through the interlensar sclera as a cylindrical ring and ends abruptly on the inner surface of the sclera. This structure was correctly described by Lindström in *P. macrophthalmus* (1901, p. 65, pl. 6, figs. 3–5). The membranous cylinder is here termed the *intrasccleral membrane*. It is always coaxial with the sublensar alveolus and is separated from the latter by a thin layer of sclera.

The horizontal section illustrated (text-fig. 1 *a, c*, Pl. 99, figs. 1, 3) cuts through a lens in the 14th dorso-ventral file, which carries clear traces of a sublensar structure. Here the intrasccleral membrane continues below the inner margin of the sclera to form a slightly tapering flat-based cylinder; the membrane is ruptured in one place. There are two interpretations of this structure. Either, it could be a structure analogous to the crystalline cone of recent arthropods, in which case the photoreceptive organs must have lain below it, or simply a membrane within which these organs were contained. It has been shown by Exner (1891) that whereas in insects the crystalline cones are quite hard and rigid structures, those of marine arthropods are often gelatinous. If the cones of phacopids were likewise gelatinous, decay or rupture of the delicate membrane investing them would destroy them entirely. This seems to have happened in most cases for sometimes loose ends of the membrane can be seen projecting from the inner surface of the sclera in *P. fecundus* and in other phacopids. Preservation of the membrane entire would certainly be a rare event. Within the lumen of the eye are a number of branching cylindrical tubes, possibly of algal origin. One of these tubes lies directly below the base of the only preserved cone, and may have protected it from decay.

Lindström observed fine vertical threads below the lenses of *Dalmanites vulgaris* (Lindström 1901, pl. 3, fig. 50), but they are unlike the structure described here. He did not think that they were organic in origin. Likewise the hexahedral calcite crystals below the lenses of *P. quadrilineata* (ibid., p. 15, fig. 38) were not considered as having any relationship to the original structure of the eye.

Nearly all modern arthropods have crystalline cones located below the lenses in a position analogous to that of *P. fecundus*. Acone eyes were described in *Lepisma* and other arthropods by Hesse (1901), but even in these primitive types there are nevertheless large transparent refractile Semper cells below the lenses though they are not actually modified into cones. Cones are even present in arthropods with disjunct spherical lenses, such as the copepod *Pontella*, described by Parker (1891) and some sort

of cone-like refractile organ below the lens seems to be fundamental to the structure of the compound eye. Lindström believed that cones were originally present in trilobites, but had not been preserved because of their delicate nature. The opposite point of view should also be considered. In most recent arthropods the outer 'cornea' is very thin and is usually almost flat. In such cases, it can have served only as a transparent protective window, whose sole function was to let light through to the refractile cones below. It may have been possible that the corneal membrane of schizochroal trilobite eyes had a similar function and that the thick biconvex lenses would have dispensed with the need for cones. These lenses and the cones of recent arthropods might have had an identical function. The division of the lenses into an outer crescentic and an inner elliptical region (see p. 610) might indicate differences in refractive index within the lens, thus all necessary refraction may have been effected within the lens.

In those recent arthropods with truly biconvex lenses (e.g. *Oniscus*, described by Debaisieux 1944), the lenses do, however, have cones, and they must therefore have been essential in such cases. The weight of evidence would indicate that the sublensar structure described here is indeed the equivalent of the crystalline cone of recent arthropods. If this is so, then the photoreceptive organs would need to be located below the bases of such cones, and in *P. fecundus* there is adequate space in which to accommodate them. The only other organ necessary within the eye is the optic ganglion, and even if this was of fair dimensions, as is common in eyes of the apposition type (see below), relatively long ommatidia could nevertheless have been present.

2. Structures seen in vertical section

Progressive grinding of the right eye resulted in sections being exposed through several complete dorso-ventral files (text-fig. 1 *d-i*, Pl. 99, fig. 2). These sections were usually made normal to the outer surface of the eye, but one or two were deliberately ground askew to show the nature of lens/scleral contacts in oblique section.

As each lens is situated at the top of a sublensar alveolus the lenses are separated by thin scleral projections. The intrascleral membranes of each lens appear very close together in these sections. The scleral projections are thin between the principal planes of the lenses, widening out above and below this level and they all have square-cut ends. A curious and unexpected feature is that these projections are all virtually horizontal and parallel with each other rather than being radially divergent, even though the lenses and particularly the uppermost ones may be inclined at an angle to them. In the specimens examined the palpebral lobes were broken, but in row 13 the upper lens belongs to the upper horizontal row and the same condition appears. This parallel arrangement applies both to the scleral projections themselves and to the intrascleral membranes running through them. It is unlikely to be the result of freak preservation, as it is found in other phacopids also. In *Reedops cephalotes* (Barrande) a similar condition has been noted in an eye with ten lenses per file; all the scleral projections are parallel. The functional significance of this structural pattern is difficult to assess, though some comments are appended below.

Phacops latifrons (Bronn)

Text-fig. 2 *a-g*. Plate 99, figs. 4-7

P. latifrons possesses an eye similar to that of *P. fecundus*, but it is larger relative to

the cephalon, and the lenses are more deeply sunken within the interlensar sclera. Burmeister (1846, p. 89, pl. 4, fig. 12) figured the eye, and Clarkson (1966c, p. 474) has briefly commented upon the external morphology, but variation within the eyes of this species has not yet been worked out in detail. Barrande (1852, pl. 3, fig. 16) illustrated a partly weathered eye exhibiting the effects of erosion which removed the outer parts of the lenses but left central stumps (noyaux).

All specimens sectioned came from Gerolstein, Eifel, North Germany. Horizontal sections were cut from both eyes of specimen no. 20607, vertical sections from both eyes of no. 20584 and from the left eye of no. 20576. The right eye of the latter was damaged.

In no. 20607, which is quite typical of the species, the maximum lens diameter was 0.375 mm. There were 17 dorso-ventral files with a maximum of 5 lenses per file. The lens distribution was as follows:

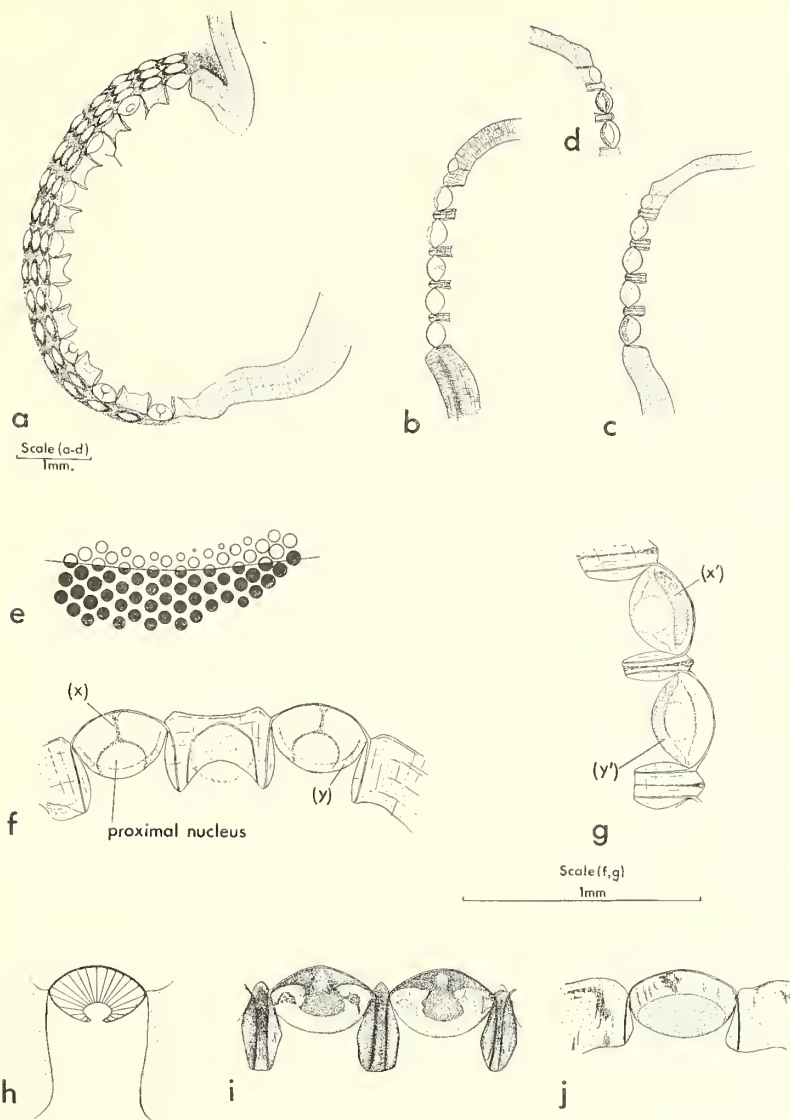
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The principal differences from *P. fecundus* are as follows. The dorso-ventral files diverge downwards at a lesser angle, thus the horizontal sections include almost complete horizontal rows without the peripheral interpolation of the lenses of adjacent rows (text-fig. 2a, Pl. 99, fig. 4). In these sections the inner surface of the interlensar sclera is indented between the lenses rather than planar as in *P. fecundus* but is otherwise similar. The palpebral lobes of *P. latifrons* were intact and the complete sections show that all the scleral prolongations are parallel. There are no traces of sublensar structure. As previously noted, internal structures in the lenses of *P. fecundus* were not very clear though distinct traces of a proximally placed 'nucleus' were visible in some of the lenses. The intralensar structures of *P. latifrons* are better preserved, though recrystallization of calcite within the lenses has resulted in the partial obliteration of the elements originally present. As not all the lenses have been preserved in the same way the interpretation put forward here is necessarily tentative and there is some difficulty in reconciling the internal construction according to this interpretation with the rather diverse structures reported in different species by Clarke, Lindström, and Rome.

P. rana, studied by Clarke (1889, p. 258, pl. 21, figs. 1-6, 27, redrawn in text-fig. 2h), possesses a small spherical indentation in the lower surface of each lens. This proximal cavity becomes filled with sediment after the death of the trilobite, and thus appears in section and in internal moulds as a small central boss or tubercle.

P. macrophthalmus, the best-preserved of the species studied by Lindström (1901, pp. 30-31, pl. 6, fig. 5, redrawn in text-fig. 2i), has lenses with an upper mushroom-shaped unit interlocking with a lower bowl-shaped structure. There is no trace of a proximal cavity in this or any of Lindström's species. Lindström suggested that the lenses originally consisted of thin layers, arched downwards below and upwards above, as in the eyes of recent crustaceans and spiders.

Rome's figures (1936, p. 4, pl. 2, figs. 9-12, redrawn in text-fig. 2j) of the eye of *P. accipitrinus maretioleensis* illustrate lenses with an outer crescentic part enclosing a smaller inner proximal region. The difference between this structure and that of *P. rana* is that the proximal region in *P. accipitrinus maretioleensis* is larger and seems actually to be an intrinsic part of the lens, and not merely a cavity within it.



TEXT-FIG. 2. *a-g*. Anatomy of the eye of *Phacops latifrons* (Bronn). *a*, Horizontal section through the left eye of Grant Institute no. 20607 along the line shown in fig. *e*. $\times 10$. Internal structures can be seen in some of the lenses. *b*, Section through 6th file of left eye, no. 20576. The section was cut slightly askew and does not pass through all the lens-centres. $\times 10$. *c*, Vertical section of file 5, right eye, of no. 20584. $\times 10$. *d*, Vertical section of file 5, left eye, no. 20584. $\times 10$. *e*, Line of section in fig. *a*, no. 20607. $\times 5$. *f*, Enlargement of two lenses of the rear part of the eye in fig. *a*, left eye, no. 20607. The lenses each display a proximal nucleus, and above this a thin median strand (*x*) running normal to the upper surface as well as traces of layering in the lower parts (*y*). $\times 40$. *g*, Enlargement of part of fig. *d*. Left eye, no. 20584. $\times 40$. This section is cut diagonally and thus passes directly through the centre of the proximal nucleus in the upper lens, but slightly to one side of it in the lower. The crescentic strip in the upper lens, (*x'*) may be the equivalent of the median strand (*x*) in the horizontal section in fig. *f*, in this case cut sagittally. *h*, *Phacops rana* (Green). Schematic representation of lens structure, redrawn from Clarke (1889) (not to scale). *i*, *Phacops macrophthalmus* Burmeister. Vertical section through a dorso-ventral file, redrawn from Lindström (1901) (not to scale). *j*, *Phacops accipitrinus maretioleensis* (R. and E. Richter), redrawn from Rome (1936) (not to scale).

The original structure of the lenses of both species may have been the same, but in *P. rana* the lower margins of the lenses have been disrupted so as to let in sediment which filled the proximal cavity when the original contents had disappeared, whereas in *P. accipitrinus maretolensis* the lenses were left intact and the contents of the proximal cavity could not be removed. It is probable that the latter were originally gelatinous.

In *P. latifrons* some lenses show distinct indications of a spherical proximal nucleus surrounded by an outer crescentic region (text-fig. 2*f*, *g*, Pl. 99, figs. 4, 6). Normally the two regions are separated by a thin dark line but do not show major compositional differences. There is no evidence that the proximal nucleus is actually a cavity connected with the sublensar alveolus for the inferior rims of the lenses are never indented. Barrande's figure showing the weathered surface of an eye of *P. latifrons*, already referred to, shows correctly the nature of the central lens-nuclei (noyaux) which are part of the original structure of the lenses rather than intralensar continuations of the sublensar alveoli. The proximal nucleus of this species is evidently similar to, but smaller than, that described by Rome.

Some sections, cut in the vertical plane, show an additional kind of proximal structure, in the form of a thin downwardly convex layer of transparent calcite, following the lower surface of the lens and separated from the upper regions by a distinct compositional change (text-fig. 2*f* (*y*), *g* (*y'*), Pl. 99, figs. 5, 7). The proximal nucleus lies in a central indentation in the upper surface of this layer and abuts directly against the lower margin of the lens. Whilst the existence of the proximal nucleus and the thin proximal layer just described seem to be well established, there are still some uncertainties in interpreting the remaining structures.

Horizontal sections of both the eyes sectioned show certain lenses with thin medial strands co-directional with the lens-axes (text-fig. 2*f* (*x*), Pl. 99, fig. 6) and extending from the proximal nucleus to the upper surface. These were only visible in some of the lenses but, where present, they seemed to be persistent throughout each lens as the eye was ground down horizontally.

Vertical sections, on the other hand, show some lenses with an apparently different internal constitution. Two such lenses are illustrated in sections through different files of specimen no. 20584 (text. fig. 2*c*, *d*, *g*, Pl. 99, figs. 5, 7). Each of the sections illustrated was ground normal to the surface along the length of the file but somewhat diagonally and not through the centres of all the lenses. The internal structures only appeared in their entirety where the section passed through the median vertical plane of each lens. In such cases a regularly arched mass or plate of transparent calcite (*x'*), was seen overlying the proximal nucleus, parallel with the upper surface of the lens (text-fig. 2*c*, *d*, *g*). It is possible that the structures here shown as *x* and *x'*, appearing in different planes, are in fact different views of the same type of intralensar organ which can be interpreted as a medial vertical plate, dividing the upper part of the lens, above the nucleus, into two regions. This bipartite effect may be the result of the original secretion of the lens by two underlying cells, but may also be part of a mechanism for concentrating light as it passed through the lens. If the proximal nucleus was of higher refractive index than the rest of the lens it could in itself have acted as a discrete source transmitting light received from above to the deeper-lying photo-receptors

PHYSIOLOGICAL CONSIDERATIONS

1. *Sublensar ommatidial arrangement*

Though no traces of sublensar ommatidial structure are preserved apart from the 'cone' already described in *P. fecundus*, it is nevertheless possible to infer much about the deep-lying structural arrangement of the eyes of both species from the directions of the sublensar alveoli and the intrascleral membranes alone.

It is important first to note, for comparative purposes, the main ommatidial types present in modern arthropods. There are only two basic types of ommatidial element, defined by Exner (1891) as apposition and superposition ommatidia.

Eyes with apposition ommatidia ('apposition eyes') are perhaps the simplest kind. They are characteristic of diurnal arthropods living in bright light. The photoreceptive units (rhabdoms) of the ommatidia are very long and extend from the base of the crystalline cone to the basement membrane of the eye. Each ommatidium is virtually isolated from its neighbours by screening pigment.

'Superposition eyes' are typical of nocturnal and crepuscular arthropods. The rhabdom of a superposition ommatidium is short and swollen, extending only a third of the total distance from the basement membrane to the cone, and connected to the latter by a thin cone-stalk. In daylight screening pigment effectively isolates each ommatidium, but in dim light this pigment migrates towards the upper and lower ends of the ommatidia, so that light can pass through the translucent ommatidial walls. Thus individual rhabdoms may be illuminated by light passing through many lenses. This device apparently increases the light sensitivity of the eye, though definition may be lost. There is, however, no clear agreement over many points in the differential physiology of the two kinds of eye. Full and detailed accounts of apposition and superposition are given in Waterman (1961) and Goldsmith (1964).

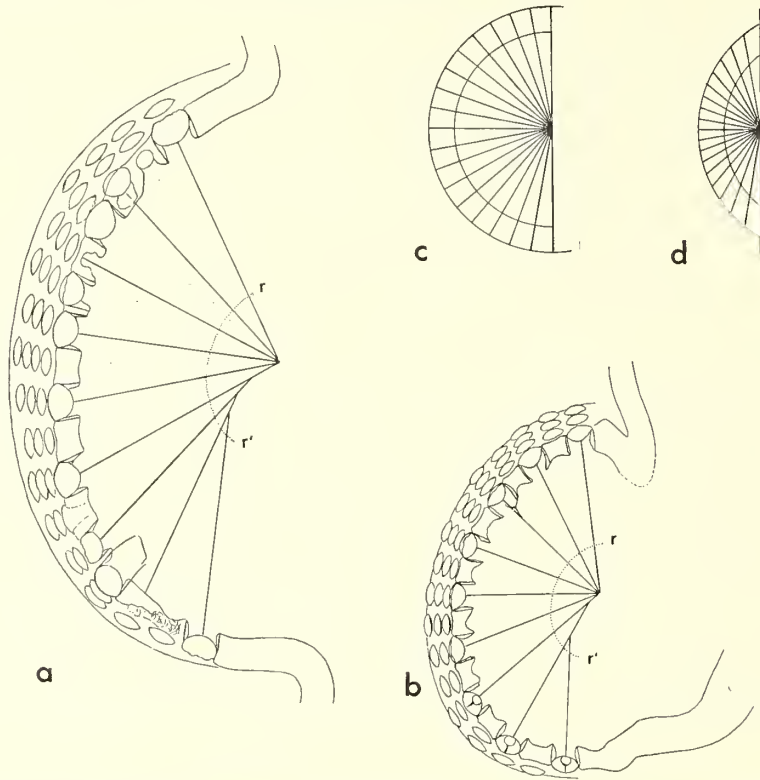
This information on the two basic eye-types is useful in interpreting the possible sublensar structures in *Phacops*, especially in their horizontal arrangement.

(a) *Horizontal arrangement.* In horizontal sections the sublensar alveoli show a markedly radial pattern, which must indicate an originally radial ommatidial arrangement. Diagrams (text-fig. 3 *a, b*) show the inferred directions of the ommatidial axes, which are taken as having lain vertically below, and parallel with, the sublensar alveoli and intrascleral membranes. Lines were drawn from the centre of each lens of the horizontal row in question in directions given by the walls of the alveoli. (Where the lens does not appear on the section owing to the curvature of the horizontal rows, directions could be surmised from the arrangement of neighbouring lenses.) As in the insect eyes described by del Portillo (1936), using a somewhat similar method, these lines do not all converge to a single point. Projected ommatidial axes of the central and anterior lenses are perfectly convergent, but those of the more posterior lenses lie on a curve, the 'Brennkurve' or curve-of-focus of del Portillo. They are shorter than the anterior axes. The differential curvature of the visual surface which is mainly responsible for this phenomenon results in a larger number of lenses covering the anterior part of the visual field (Clarkson 1966c, text-fig. 3); a situation which is presumably of some adaptive significance.

All the ommatidial axes converge to a point or region whose distance is less than that

from the surface to the centre of curvature of the eye. Thus the peripheral ommatidia are not normal to the visual surface.

To show the significance of this feature two simple theoretical models are illustrated showing different types of radial ommatidial arrangement.



TEXT-FIG. 3. Internal arrangement of the visual units. *a. Phacops fecundus* Barrande. Grant Institute no. 20575. Horizontal section as in text-fig. 1*a*. Diagram illustrating original internal arrangement of the ommatidia, as inferred from the directions of the sublensar alveoli. The lines represent ommatidial axes. A possible maximum depth for the basement membrane is given by the line rr' . *b. Phacops latifrons* (Bronn). Grant Institute no. 20607. Horizontal section as in text-fig. 2*a*. Inferred ommatidial arrangement, as above. *c*, Model of an arthropod eye where the ommatidial axes converge to the centre of surface curvature. *d*, Model of an eye where the axes converge to a point only half the depth of the centre of surface curvature. This more nearly approximates the phacopid condition.

The first model (text-fig. 3*c*) shows an eye with a perfectly hemispherical surface, having ommatidia whose axes all converge to a point at the same locus as the centre of curvature of the visual surface. Eyes of this type are not uncommon in arthropods and are usually associated with superposition-type ommatidia. The second model (text-fig. 3*d*) is more similar to those of *P. fecundus* and *P. latifrons* but is regularly curved. The point of axial convergence is only half the distance from the surface to the centre of curvature. Eyes of such a type usually have apposition-type ommatidia. An eye

of the latter type can accommodate as many ommatidia with the same axial separations, and subtending as great a visual range as can one of the former variety, unless the ommatidia are very long. If they are long they can only be housed internally by reducing the length of the central ommatidia relative to the peripheral ones.

Although it is not possible to infer the maximum depth of the ommatidia and hence the basement membrane in *P. fecundus* and *P. latifrons*, it cannot, at its maximum, have been as deep as the region of internal convergence of the anterior lenses. In text-fig. 3a, b, the line rr' shows the deepest possible position for both species which would allow room for a small optic ganglion. It is probable, however, that the ommatidia were somewhat shorter than this.

Although some superposition eyes have an irregularly curved surface, the majority approximate the ideal condition of text-fig. 3c, in order that they may function efficiently for night-vision in the manner described by Exner (1891). The principal advantage of the second model, where the eye is not of superposition type, is that the same organs may be more efficiently stowed inside the eye. Less of the eye projects, giving greater protection, and there is less internal wasted space. Only enough room is needed below the ommatidia to accommodate the optic ganglion, thus to some extent the degree of curvature of the visual surface must depend on the size of the latter.

These considerations upon the original internal anatomy of the eye bear upon the differentiation in lens size observed in *P. fecundus*, *P. latifrons*, and most other phacopids. The ommatidia or visual units of a single eye may be assumed to have been of similar construction and shape. Large lenses must be associated with large ommatidia, and small lenses with smaller and, as ommatidia of all sizes are of identical form, consequently shorter ommatidia. Thus the peripheral large lenses of *P. fecundus* and *P. latifrons* indicate deeper ommatidia, and the smaller central ones similar though shorter ones. These conditions may be compared directly with the hypothetical second model (text-fig. 3d), which exhibits a very similar structure. It is possible that the ancestral phacopid eye approximated this form. In phacopids derived from such an ancestor, differential curvature of the visual surface relating to distinct visual adaptations was superimposed upon it; many of these adaptations have been previously described (Clarkson 1966c).

Summarizing, there is some evidence that the ommatidia of *P. fecundus* and *P. latifrons* were moderately long. In the horizontal plane they were arranged radially, though the outer lenses were not normal to the surface. This arrangement would almost certainly preclude any superposition image being formed. The eye could only have functioned as an apposition eye, and the internal structures reflect adaptation to apposition-type vision, with maximum economy of spacing internally as many ommatidia as could be accommodated in a superposition eye of much greater size.

(b) *Vertical arrangement.* The physiological significance of the parallel arrangement of ommatidia in vertical section is obscure.

As far as the author is aware, nothing quite like this pattern exists in the laterally directed eyes of recent arthropods. The nearest approximation is found in certain deep-water euphausiids. In these (Chun 1896, Kampa 1965) each eye is divided into two isolated lobes, the upper of which is directly forwards and upwards, whereas the lower has a downward and backward orientation. The ommatidia of the lower lobe

are radially arranged, but in the upper lobe they are all parallel. In contrast with phacopids, this parallel arrangement is constant in both sagittal and transverse planes, so that the lobe consists, in effect, of numerous ommatidia all pointing in the same direction. But as in phacopids, these parallel units with their large cones lie below a curving visual surface and individually are capped by strongly convex corneal 'facets'. In view of these structural similarities, a certain degree of physiological interpretation of the phacopid eye might be made with reference to that of the euphausiids, but little is known of the essential physiological attributes of the eyes of the latter, such as their angular light-receptivity, which would be of value in this case.

The structural dissimilarities furthermore, may outweigh the similarities and thus preclude fruitful comparison. Not only is the phacopid eye a laterally, rather than upwardly directed organ, but the visual units of phacopids are parallel only in the vertical plane. Likewise, there is no pigment between the ommatidia of the euphausiid upper lobe and thus no isolation of the visual units, but in the phacopids, prolongation of the sclera between the lenses must inevitably isolate the ommatidia. Finally, the lenses of phacopids are immensely larger than those of the euphausiids.

The eyes of these euphausiids are highly modified, and are adapted to function in deep-water conditions where bioluminescence and dim illumination from above are the only light sources. The resemblance between these eyes and those of phacopids may not be entirely fortuitous, but one cannot go further at present with this particular topic.

A possible explanation of the parallel arrangement of the visual units would relate it to different adaptations to day and night vision. In recent arthropods, such adaptations are controlled by internal movements of pigment, but the presence of pigments in trilobites is not known, though they may well have existed.

The externally directed optic axis of each lens defines the centre of its cone of vision. As the outer lens-surfaces are strongly convex, the cones of vision must have been relatively wide, though as in *Limulus* (see Waterman 1954) the threshold of visual stimulation probably increased away from the axis. Hence though the eye is adapted to receive light from the whole visual field, i.e. the region covered by all the lens axes, and its penumbra (Clarkson 1966a), it is also directly susceptible to horizontal light rays, parallel with the ommatidial axes. These rays would pass at an angle through the lens, but straight towards the photoreceptors with little change in direction. As shown below, they may have effected total internal reflection within the cone, if the latter were of high refractive index.

In this way the dorso-ventral files would have a similar function to those of *Acaste downingiae*, where their lens-axes form widely separated visual strips, capable of detecting the movement of bottom-living animals. Such a mechanism would mainly be effective in daylight on a brightly illuminated sea-floor. During daylight also there would presumably be some side effect from the weaker illumination above the sea-floor, but at night or in twilight, when the sea-bed became dark, illumination from above was the only available light.

The strong convexity, large size, and high angular separation of the lenses enabled this dim light to be received over a wide visual range, and thus would give a reasonable degree of night vision. This was probably supplemented by pigment migrations.

2. *Transmission of light to the deep-lying photoreceptors*

In both horizontal and vertical sections there is a definite discrepancy between the angular bearings of the lens-axes and the inward directions of their associated ommatidia, as inferred from the courses of the sublensar alveoli. The eye is adapted to gather light from a particular region of the trilobite's external environment and this adaptation controls the external bearing of the lens axes. The internal arrangement of the ommatidia facilitates maximum spatial economy for the number and size of the ommatidia, and may also, as already explained, be related to the possibility of day and night vision.

Thus the collection of light from the external environment and its internal transmission to the photoreceptors are controlled by a number of factors, and in order that all requirements are satisfied a change in the direction of light within the eye may be necessary.

Exactly how this is accomplished is a problem which can only be discussed in a theoretical sense, though there are three or more factors involved.

(i) In *P. fecundus* extreme discordance between the direction of the external optic axis and sublensar alveolus is often associated with the bulging of the lower surface of the lens in the direction of the ommatidial axis. The optic axis of the lens seems to be bent below the principal plane, which might result in an intralensar change in light direction.

(ii) *P. latifrons* has lenses internally differentiated into two regions. The proximal nucleus may have had a higher refractive index, and light would then be trapped within it. The base of this nucleus would then act as a discrete internal light source, transmitting light in all directions including the line of the ommatidial axis. Pigment screening would effectually trap most of this available light within the ommatidial cylinder, resulting in the stimulation of the photoreceptors. As far as can be made out, the intralensar structures in *P. fecundus* would work in the same way.

(iii) A third possibility involves total internal reflection within the cone, if the latter had a high refractive index. Numerous authors working with recent arthropods have suggested that this simple and well-known physical phenomenon might have the effect of trapping light within the crystalline cone and guiding it towards its appropriate light-accepting organ. Many examples taken from insects were cited by Goldsmith (1964), and Kampa (1963, p. 77) has suggested the possibility in a crustacean. Confinement of light within phacopid cones and its subsequent transmission to the deeper-lying photoreceptors could account for the necessary internal change in light direction.

Further physiological studies on trilobite vision must be delayed until the internal structures of other eyes have been investigated.

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THE HYSTERO-ONTOGENY OF *LONSDALEIA* McCOY AND *THYSANOPHYLLUM ORIENTALE* THOMSON

by R. K. JULL

ABSTRACT. Increase in thirteen specimens of *Lonsdaleia* and two of *Thysanophyllum orientale* from Great Britain was studied by means of closely spaced acetate peel sections. With the exception of one example of inter-mural increase, only lateral increase was observed. *Lonsdaleia* is characterized during early development by having a long cardinal septum, the axial end of which forms the median lamella of the axial structure. Septal insertion is at first of the zaphrentid mode but subsequently becomes variable, depending on the development of minor septa. Most daughter corallites are radially orientated to the parent, but some are tangential. Interseptal dissepiments are typically formed first, followed by their modification to lonsdaleoid dissepiments.

Development in *Thysanophyllum orientale*, type species of *Thysanophyllum*, resembles that in *Lonsdaleia* in the nature of the cardinal septum and dissepimental development. These characters, together with the presence in a few adult corallites of *T. orientale* of a weakly developed axial structure suggest that *Thysanophyllum* is related to the Lonsdaleiidae rather than the Lithostrotionidae as has been suggested by some workers.

SOME of the taxonomic problems resulting from the morphologic variation of rugose corals have not been satisfactorily solved by the standard technique of examining adult characters alone. Such difficulties exist as regards the family affinities of *Thysanophyllum* Nicholson and Thomson, a widely distributed genus of Carboniferous and Permian age which lacks an axial structure and has short septa and lonsdaleoid dissepiments (Pl. 102, figs. 5a–b). Some workers (Lecompte 1952, Hill 1956, Fedorowski 1965) regard this genus as being a diphymorphic lonsdaleoid and thus place it with the Lonsdaleiidae. Others, however (Minato 1955, Easton 1960, Fontaine 1961, Soshkina and Dobrolyubova 1962), assign it to the Lithostrotionidae partly since corallites of *Lithostrotion* Fleming may lack an axial structure and possess lonsdaleoid dissepiments, thus closely resembling the characters of *Thysanophyllum*.

A solution to this problem is attempted here by a study of closely spaced acetate peel sections of the characters of increase in thirteen specimens of *Lonsdaleia* and two of *Thysanophyllum orientale*, type species of *Thysanophyllum*. These specimens, which are listed in text-fig. 1, are all from Viséan beds in Great Britain. From a comparison of the hystero-ontogeny of *Thysanophyllum orientale* with that in *Lithostrotion* (see Jull 1965) and *Lonsdaleia*, typical genera respectively of the Lithostrotionidae and Lonsdaleiidae, it is concluded that *Thysanophyllum* is probably related to the Lonsdaleiidae.

Observations of hystero-corallite development range from the start of increase up to the late neanic stage and sometimes the ephebic stage. Crushing in three coralla has destroyed the early stages of development in some or all of the corallites studied.

The terminology applied by Jull (1965) to increase in *Lithostrotion* is used herein. Abbreviations associated with catalogue numbers are as follows: BM—British Museum (Natural History), London; RSM—Royal Scottish Museum, Edinburgh; UQ—Department of Geology and Mineralogy, University of Queensland, Brisbane.

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Name	Number	Locality	Zonal age	Corallites studied	Remarks
<i>Lonsdaleia duplicata duplicata</i> (Martin)	BM R1366	Corwen, North Wales	D ₂ -D ₃	4	
	RSM 1878.11.267	Hafod, near Corwen, North Wales	D ₂ -D ₃	3	early stages crushed
<i>L. floriformis floriformis</i> (Martin)	UQ F11035	Wrekin, Shropshire	D ₂	1	diphymorphic corallites
	UQ F2961	Pen-y-ghent, Yorkshire	D ₂ -D ₃	3	
	RSM 1966.6.1	Coldstone Quarries, Greenhow, Pately Bridge, Yorkshire	D ₂	8	
	BM R17160	Coalbrookdale, Shropshire	D ₂	5	
	BM R24850	Longstone Edge, north of Bakewell, Derbyshire	D ₂	2	diphymorphic corallites
<i>L. floriformis crassiconus</i> McCoy	UQ F5683	Clifton, near Bristol	D ₂	8	
	RSM 1966.6.2	Gathorn Plain, Orton, Westmorland	D ₂	14	
	BM R16995	Avon Gorge, Bristol	D ₂	17	topotype
	BM R16997	Avon Gorge, Bristol	D ₂	13	topotype
<i>L. floriformis near laticlavata</i> Smith	BM R36865	Oswestry, Shropshire	D ₂ -D ₃	3	
<i>L. caledonia</i> Smith	RSM 1966.6.3	Coalburn, Lesmahagow, Lanarkshire, Scotland	D ₂	3	early stages crushed
<i>Thysanophyllum orientale</i> Thomson	UQ F46767	Aberlady Bay, East Lothian, Scotland	Coral Zone 3	6	topotype
	RSM 1966.6.4	West Kirkton Quarry, Bathgate, West Lothian, Scotland	Coral Zone 3	7	early stages crushed in 3

TEXT-FIG. 1. Specimens of *Lonsdaleia* McCoy and *Thysanophyllum orientale* Thomson studied by means of closely spaced acetate peel sections.

INCREASE IN *LONSDALEIA*

Studies of increase in Lower Carboniferous representatives of *Lonsdaleia* have been made by thin section examination of British material by Smith (1916) and on material from the Russian Platform by Dobrolyubova (1958). Fedorowski (1965) described development in two Lower Permian species of *Lonsdaleia* from Hornsund, Vestspitsbergen, using serial acetate peel sections. These studies include a large number of species but there are nevertheless significant aspects of the hystero-ontogeny requiring clarification. These are mainly: (1) the orientation of the axial plane of the daughter corallite with respect to the axis of the parent; (2) the manner of development of lonsdaleoid dissepiments; (3) the pattern of septal insertion; and (4) the nature of the wall dividing

the daughter from the parent corallite. These characters, together with present and past knowledge of other characters, are dealt with in turn in the following discussion. Species are discussed collectively since there generally seems to be little fundamental difference between their hystero-ontogenies. As text-fig. 1 indicates, most of the observations are made on *L. floriformis floriformis* and *L. floriformis crassiconus*. Complete details of increase were obtained from only one specimen each of *L. floriformis* near *laticlavata* and *L. duplicata duplicata*, and the early characters of development are unknown in *L. caledonia*.

Mode of increase. This is almost invariably lateral in nature with the daughter corallite arising in the lonsdaleoid dissepimentarium of the parent in no preferred position with respect to the axial plane of the parent. Commonly as many as five daughter corallites may develop nearly simultaneously from the same parent (Pl. 102, fig. 2), especially in the proximal and lateral parts of the corallum. The rate of corallite development in cerioid species varies greatly but usually about 20–30 mm. of growth occurs between the start of development and the achievement of the ephebic stage. Development in the fasciculate *L. duplicata duplicata* is considerably slower, extending over some 40 mm. or more of distal growth with about 35 mm. of this occurring during late neanic development.

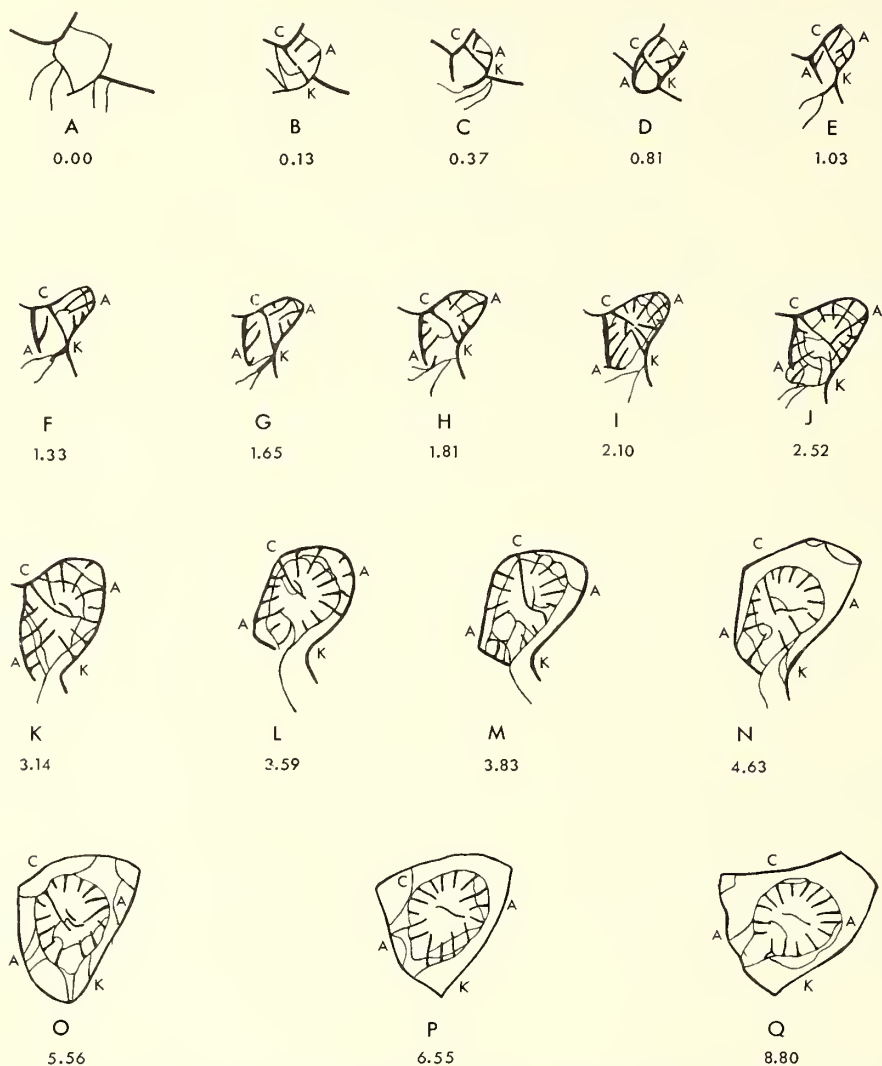
Rarely intermural increase (*sensu* Jull 1965, p. 206) also occurs whereby a youthful corallite is formed between adjacent corallites and lacks a single (obvious) parent. One example of this type of increase was observed in *L. floriformis floriformis* (text-fig. 2; Pl. 102, figs. 4*a*, *b*), and Dobrolyubova (1958, p. 79–81, pl. 9, fig. 1; text-figs. 14–16) described and illustrated this type of increase in *L. rossica rossica* Stuckenbergl from Lower Namurian C₁st beds on the Russian Platform.

Dividing wall. In all examples of increase observed, the wall which divides the daughter from the parent corallite is similar to the wall bounding adult corallites. It is formed either by thickening at the peripheral ends of parent septa (Pl. 100, figs. 2*b–f*), a character similar to that noted by Fedorowski (1965, p. 121), or by apparent modification of one or more lonsdaleoid dissepiments of the parent (corallite D3, Pl. 101, figs. 1*a–c*). When corallites of *L. duplicata duplicata* (text-fig. 4, 1*a–j*) become discontinuous, this wall is split rather than progressively disappearing as does the partition which divides daughter from parent in most fasciculate species of *Lithostrotion*.

Septal insertion. In the specimens studied, septa are inserted independently of the parent septa. Usually the cardinal septum is the first to appear and the other primary septa, the counter septum and two alar septa, may not all be present when metasepta first start to appear, especially if the dividing wall is late in forming. Insertion is of a zaphrentid nature in all quadrants (Pl. 100, figs. 2*f–j*) and this may either continue up to the ephebic stage or minor septa may appear during development and insertion alters in all quadrants to the cyathaxonid mode (Pl. 100, figs. 2*k–m*). The development of minor septa is discussed below.

In contrast to septal formation in Lower Carboniferous forms, Fedorowski (1965, p. 121) noted that the earliest septa in daughter corallites of the two Lower Permian species that he studied are formed from the detached ends of parent septa. In both species parent septa extend to the wall in the zone of increase preceding the appearance

of the daughter corallite whereas in the Lower Carboniferous forms, this zone of increase is usually free of parent septa.



TEXT-FIG. 2. Intermural increase in *Lonsdaleia floriformis floriformis* (Martin), UQ F11035. Numbers below figures are cumulative distances of distal growth in mm. Thick lines are intercorallite walls and septa; thin lines are dissepiments and tabulae. In A, the youthful corallite is formed in lonsdaleoid dissepiments and is only separated from adult corallites lying to the upper-right and lower-left by lonsdaleoid dissepiments. Neither of these adult corallites could be established as the parent. The union of axial septa in C-H is uncommon in *Lonsdaleia*. Developmental stages, of which the late neanic is the last illustrated (Q), merge into one another. $\times 4$.

Axial septa and axial structure. During early development, the cardinal septum is almost invariably the longest septum and the counter and alar septa are typically indistinguishable from metasepta. The median lamella of the axial structure is formed from the axial

end of the cardinal septum, and during the progressive appearance of tabellae and other lamellae in the axial structure, the cardinal septum may or may not remain attached to the median lamella. During the ephebic stage and later part of the late neanic stage the two are usually detached.

Dobrolyubova (1958, p. 27) did not trace septal insertion in the species which she examined but suggested that the longer septum was the cardinal septum. Smith (1916, pp. 230, 232), on the other hand, considered the longer septum to be the counter septum but he likewise did not trace septal insertion. In some of the youthful corallites which he illustrated (ibid., pl. 17, figs. 5-23), insertion appears to be taking place beside this septum, indicating that it is perhaps the cardinal septum. De Groot (1963, p. 80) remarked that an elongate cardinal septum is characteristic of lonsdaleoid genera, but Fedorowski (1965) did not note any long septum during development in his lonsdaleoid species.

Name	Number	Radial	Tan- gential	Indeter.	Total
<i>L. duplicata</i> <i>duplicata</i> (Martin)	BM R1366	2	1(?)	1	4
	RSM 1878.11.267	—	—	3	3
<i>L. floriformis</i> <i>floriformis</i> (Martin)	UQ F2961	3	—	—	3
	RSM 1966.6.1	6	1	1	8
	BM R17160	1	2	2	5
	BM R24850	2	—	—	2
<i>L. floriformis</i> <i>crassiconus</i> McCoy	UQ F5683	7	1	—	8
	RSM 1966.6.2	10	3	1	14
	BM R16995	14	1	2	17
	BM R16997	11	—	2	13
<i>L. floriformis</i> near <i>latioclavia</i> Smith	BM R36865	1	1	1	3
<i>L. caledonia</i> Smith	RSM 1966.6.3	—	—	3	3

TEXT-FIG. 3. The number of corallites with radial and tangential orientation in the specimens studied. Orientation is based on the position of the axial plane of the daughter corallite with respect to the axis of the parent. Indeterminate corallites are those in which the early stages are not preserved, usually through crushing, or the position of the axial plane could not be definitely established.

Orientation of the daughter corallite. Text-fig. 3 shows that the majority of corallites studied are radially orientated with the cardinal septum positioned on the outer side, furthest from the axis of the parent. Most of these corallites are orientated at less than 30° from a true radial orientation (Pl. 100; corallites D2 and D3, Pl. 101), a few are up to 45° away from this position (corallite D1, Pl. 101) and those that are tangentially orientated lie at from 60° to 90° away from a radial position (Pl. 102, figs. 1*a-c*; text-fig. 4, 2*a-e*). Preference to radial orientation is exemplified by those specimens in which up to five daughter corallites, all radially orientated, are ranged simultaneously around the periphery of the parent (Pl. 102, fig. 2). With one exception in which two corallites develop together, all tangentially orientated daughter corallites observed arise singly.

In many of Dobrolyubova's (1958) illustrations, the axial plane of the daughter corallite appears to be radial to the parent, but in *L. arctica* Gorsky (ibid., text-fig. 3), *L. subtilis* Dobrolyubova (ibid., text-fig. 19) and *L. floriformis floriformis* (ibid., text-fig. 12) radial orientation appears to be lacking. Possibly this may be due to the axial plane of the daughter corallite rotating during development, as I have observed in the Viséan *Aphrophyllum hallense* Smith, but this effect has not been observed in the specimens of *Lonsdaleia* here studied.

Radial orientation of the daughter to parent corallite is certainly the most common condition in *Lonsdaleia* but non-radial orientation is too common to be an abnormal occurrence. Perhaps orientation of the daughter to parent corallite is a factor of individual variation, with radial orientation being the most common tendency.

Dissepiments. The first one or two rows of dissepiments in the daughter corallite are typically formed first as interseptal dissepiments when ten or more major septa have been inserted. These are subsequently altered to lonsdaleoid dissepiments by the withdrawal of septa from the wall. In a few cases, however, lonsdaleoid dissepiments of the parent corallite are incorporated as such into the morphology of the daughter (text-fig. 4, 1*a-j*).

Minor septa. Minor septa in *Lonsdaleia* are variably developed in different specimens. In some examples of increase, especially those in which major septa are mainly confined

EXPLANATION OF PLATE 100

Numbers below Figs. 2*a-m* are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum; A = alar septum.

Figs. 1, 2. *Lonsdaleia floriformis floriformis* (Martin). 1, UQ F2961, transverse section of normal and diphyomorphic corallites, $\times 1$. 2*a-m*, lateral increase in the same specimen; *a-f*, hystero-brephic stage; *g-l*, early neanic stage, showing the appearance of the counter septum in *g* and of minor septa in *k*; *m*, late neanic stage, also showing another youthful corallite with a long cardinal septum on the right, $\times 4$.

EXPLANATION OF PLATE 101

Numbers below figures are cumulative distances of distal growth in mm. D = daughter corallite; P = parent corallite; C = cardinal septum; K = counter septum.

Figs. 1*a-h*. *Lonsdaleia floriformis crassiconus* McCoy, UQ F5683. Lateral increase in three corallites, with daughter corallites D1, D2, and D3 arising from parent corallites P1, P2, and P3 respectively. Note that the axial plane of D3 is nearly radially disposed with respect to the axis of its parent, while in D1 and D2, it is approximately 20 to 30 degrees away from a radial disposition. Minor septa in D3 appear in *f-h*, and interseptal dissepiments are formed in *d*, followed by their alteration to lonsdaleoid dissepiments in *e-g*, $\times 4$.

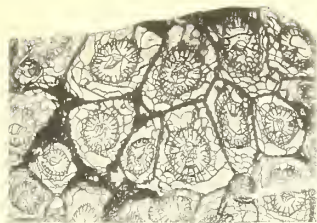
EXPLANATION OF PLATE 102

Numbers below Figs. 1*a-c* are cumulative distances of distal growth in mm. D = daughter corallite; P = parent corallite; C = cardinal septum; K = counter septum.

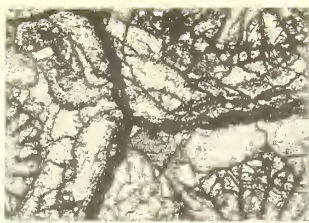
Figs. 1-3. *Lonsdaleia floriformis crassiconus* McCoy. 1*a-c*, UQ F5683, laterally arising corallite with its axial plane orientated tangential to the axis of the parent; *a, b*, early neanic stage; *c*, late neanic stage, $\times 4$. 2, BM R16997, five radially orientated daughter corallites arising from the same parent, $\times 4$. 3, transverse view of the same specimen as in Figs. 1*a-c*, $\times 1$.

Figs. 4*a, b*. *Lonsdaleia floriformis floriformis* (Martin). UQ F11035, transverse and longitudinal sections of diphyomorphic corallites, $\times 1$.

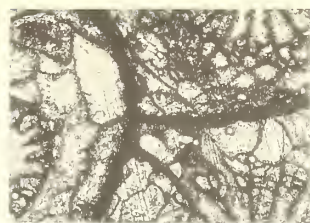
Figs. 5*a, b*. *Thysanophyllum orientale* Thomson. Topotype, UQ F46767, transverse and longitudinal sections, $\times 1$.



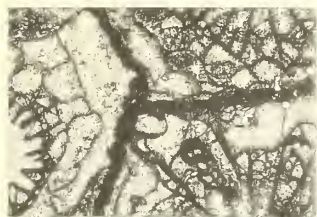
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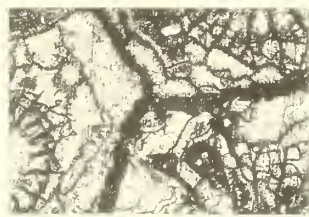
2a
0.00



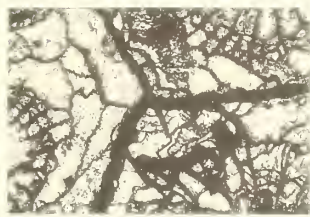
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0.60



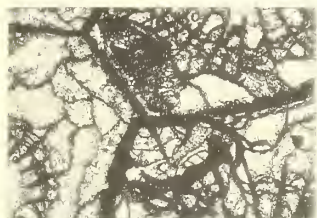
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1.40



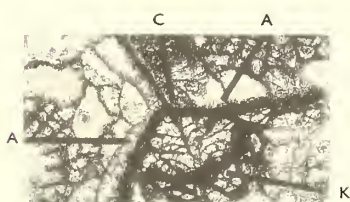
2d
1.64



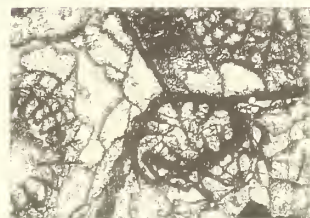
2e
1.88



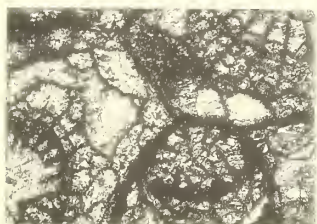
2f
2.14



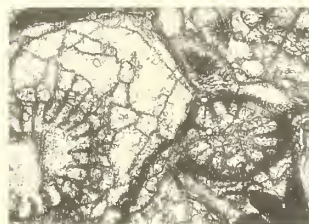
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2.44



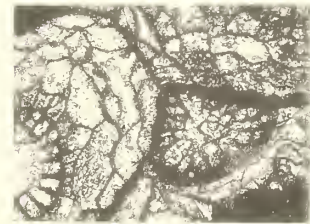
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2.58



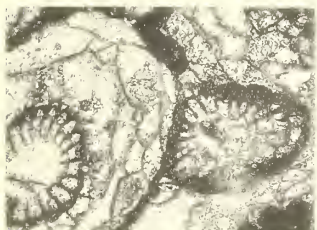
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2.74



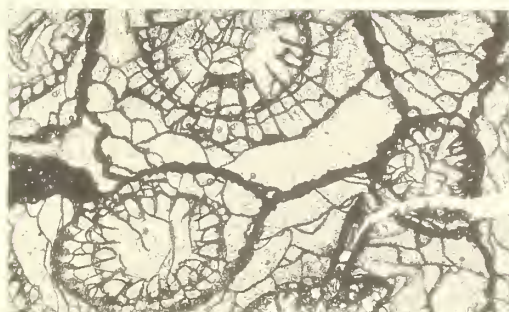
2j
2.94



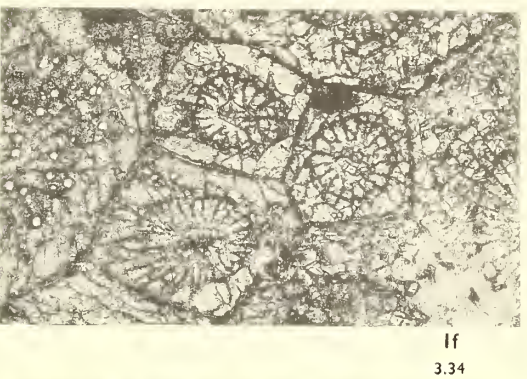
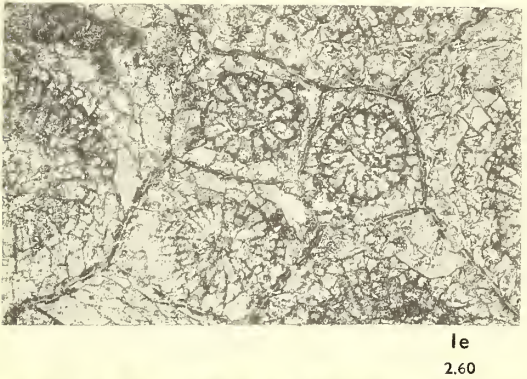
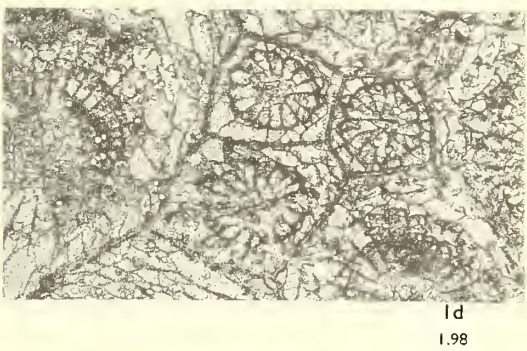
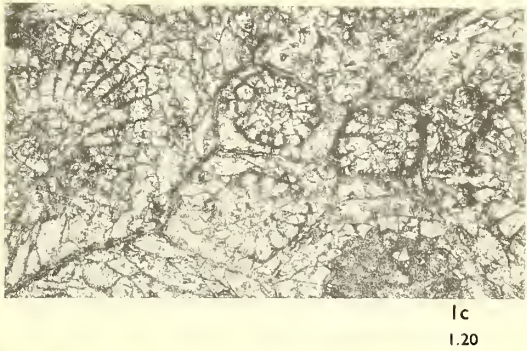
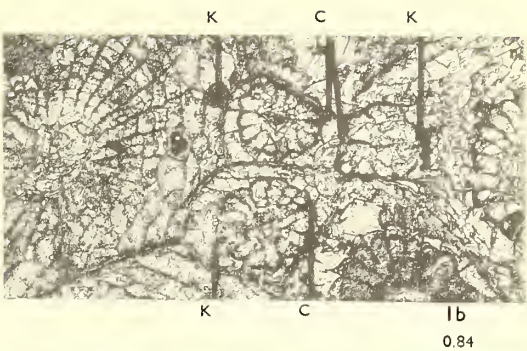
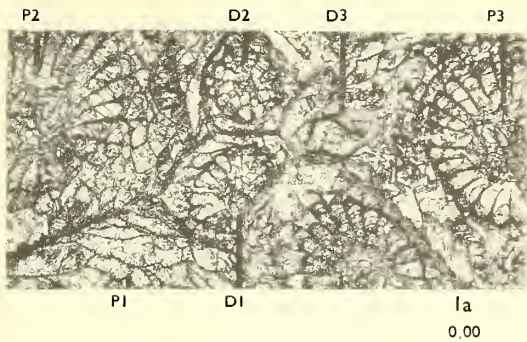
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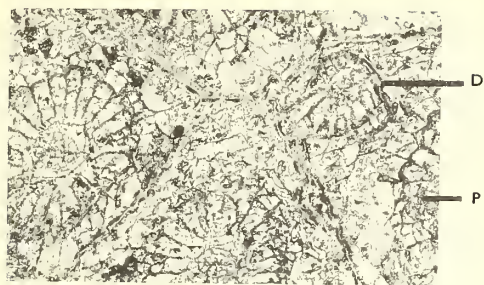


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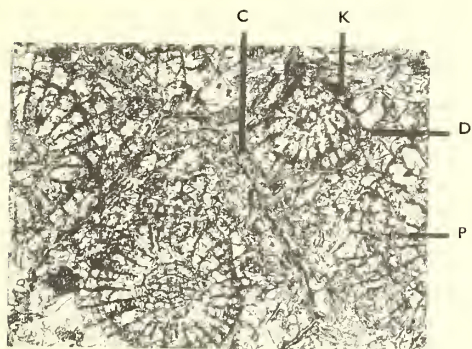


2m





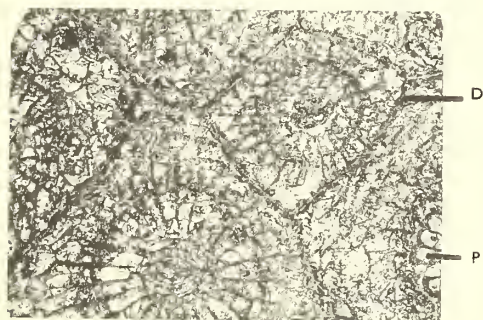
1a
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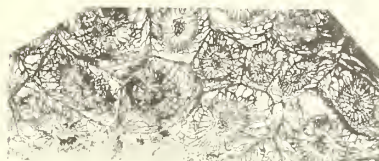
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2



1c
4.40



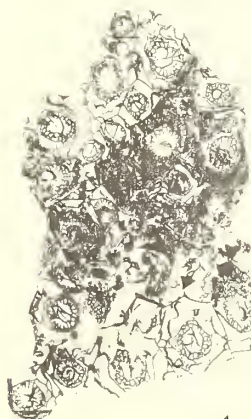
3



5a



5b

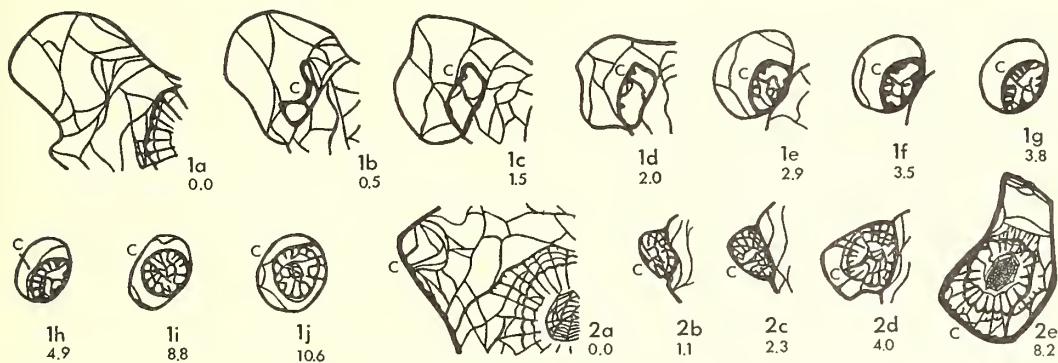


4a



4b

to the tabular area, such as in *L. duplicata duplicata* and *L. floriformis floriformis*, minor septa are absent or very short throughout hystero-ontogeny, so that insertion is entirely zaphrentid in nature. In others, however, minor septa appear as early as simultaneously with the development of the first dissepiments, in which case insertion alters to the cyathaxonid mode.



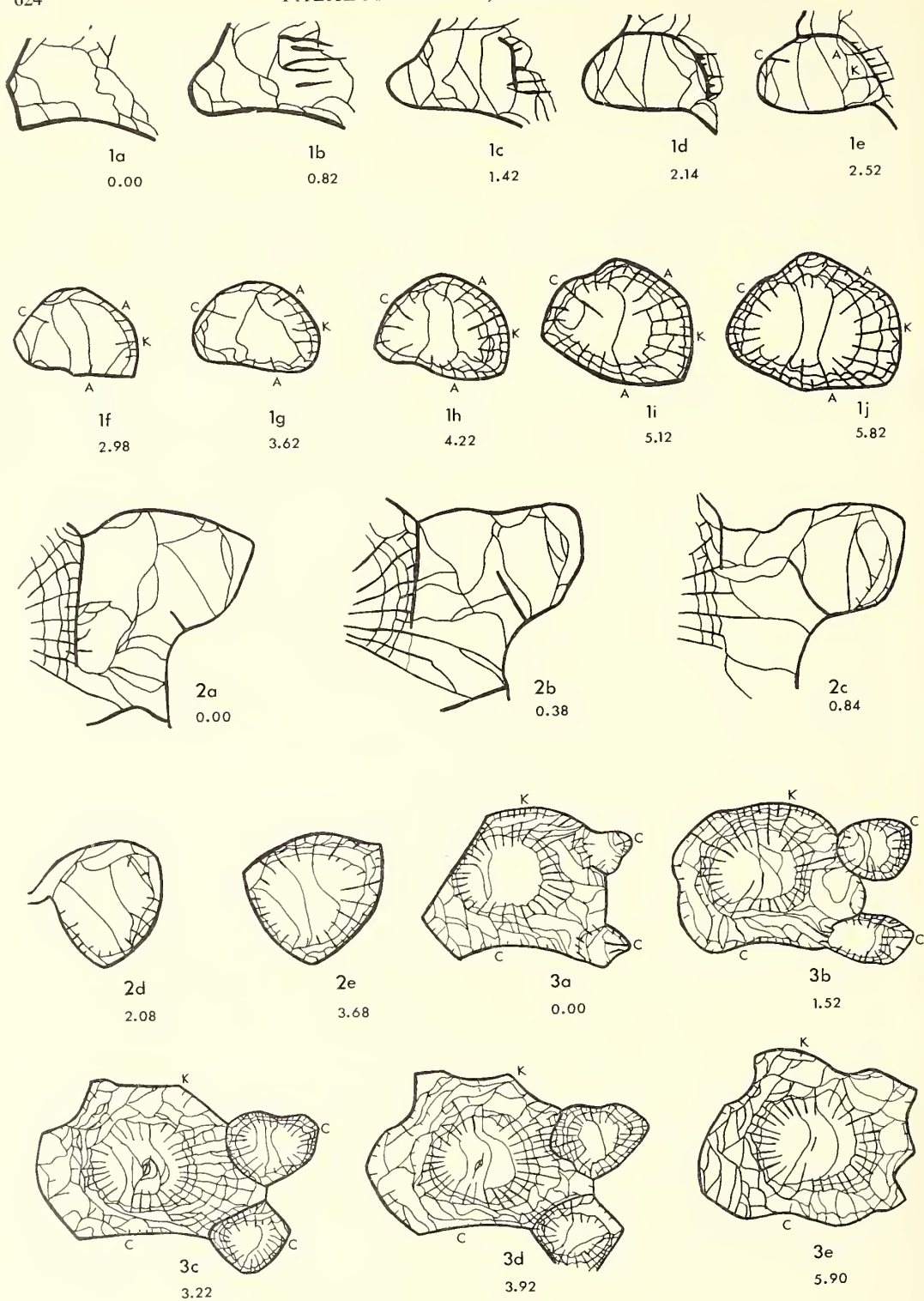
TEXT-FIG. 4. Numbers below figures are cumulative distances of distal growth in mm. C = cardinal septum. 1a-j, lateral increase in *Lonsdaleia duplicata duplicata* (Martin), BM R1366. Note that the cardinal septum extends across the corallite during early development (b-e) and that lonsdaleoid dissepiments of the parent are incorporated into the morphology of the daughter. 2a-e, lateral increase in *L. floriformis* near *laticlavata* Smith, BM R36865. Note that the daughter corallite is nearly tangentially orientated to the parent. All figures $\times 4$.

Increase in *L. floriformis crassiconus* demonstrates particularly well the variability of development of minor septa. In some corallites, few if any minor septa are inserted until a late stage of development when major septa lengthen peripherally into the lonsdaleoid dissepiments during the late neanic stage (corallite D3 on Pl. 101, figs. 1f-h); insertion is thus zaphrentid, followed by cyathaxonid. In other corallites, however, minor septa appear at an early stage of development after 10 to 15 major septa are inserted (Pl. 102, fig. 1a). These minor septa disappear where lonsdaleoid dissepiments are formed by the withdrawal of major septa from the wall, and later reappear when major septa lengthen peripherally. The pattern of septal insertion during the hystero-ontogeny of these corallites is two cycles of zaphrentid insertion alternating with cyathaxonid insertion.

The pattern of septal insertion in *Lonsdaleia* appears to be dependent to some extent on individual variation and is thus of little taxonomic importance except that the earliest mode is always zaphrentid.

INCREASE IN *THYSANOPHYLLUM ORIENTALE*

Thysanophyllum orientale, chosen by Gregory (1917, p. 238) as type species of *Thysanophyllum*, occurs in the shale of Coral Zone 3 age at Aberlady Bay, Scotland. Hill (1940, p. 162) chose as lectotype specimen 1095 in the Thomson Collection, Kelvingrove Museum, Glasgow. This specimen is one of the two syntypes from Aberlady Bay on which Thomson (1880, p. 257) based the species. Only the two specimens were known from the type locality until recently, when two additional ones were collected. One of these, RSM 1964.25, which was collected by Dr. C. D. Waterston and Mr. I. F. Sime,



is dolomitized and examination of it could only be made on polished faces. This specimen differs from the lectotype in possessing slightly larger corallites, averaging 20 mm. in diameter, and more numerous septa, numbering about 30 of each order. Part of the early and late neanic stages of development were examined in two corallites and these resemble the characters of increase described below.

The other recently collected topotype, UQ F46767, which was collected by Mr. C. P. McDonagh, yielded good serial sections of parts of the hystero-ontogeny of six corallites (text-fig. 5). Corallites in this specimen (Pl. 102, figs. 5*a, b*) are slightly larger and have a few more septa than those in the lectotype. A prominent long axial septum, which Hill (1940, p. 162) regarded as the counter septum but in all likelihood is the cardinal septum, is present in a few adult or nearly adult corallites, whereas in the lectotype only some of the youthful corallites are known to possess this long septum. Finally, some corallites in UQ F46767 have a small impersistently developed and isolated axial structure (text-fig. 5, 3*d-e*), a character unknown in the lectotype.

The other specimen studied by means of serial sections, RSM 1966.6.4, from Bathgate, West Lothian, resembles the corallum from this locality illustrated by Hill (1940, pl. 8, figs. 30-32). The hystero-ontogeny of seven corallites was studied in this specimen, but crushing has destroyed the initial stages of three of them and part of that in a fourth corallite.

Corallites arise by lateral increase in the peripheral part of the lonsdaleoid dissepimentarium of the parent. Increase normally starts with the appearance of five septa in the lonsdaleoid dissepimentarium of the parent (text-fig. 5, 1*b, 3a*). These septa correspond to the septa in the tabularium of the parent but are not united to them and they often do not terminate peripherally against lonsdaleoid dissepiments. The wall dividing daughter corallite from parent is formed near the peripheral ends of these septa, and during or following its formation these septa usually disappear.

Hystero-brephic stage (text-fig. 5, 1*d-e*). The cardinal septum is the first septum formed and the counter septum may appear shortly thereafter, or if the dividing wall is slow in being formed, it may not appear until after some metasepta have been inserted in the cardinal quadrants (text-fig. 5, 3*a*). Both axial septa are short but the cardinal septum is the longer of the two. In UQ F46767, this septum remains long throughout much of early development (text-fig. 5, 1*e-i*) but in RSM 1966.6.4 it soon shortens to equal the other septa in length. The axial plane is approximately radially orientated with respect to the axis of the parent. Alar septa may or may not be formed before metasepta appear, and are of the same length as metasepta during development. In UQ F46767 alar septa

TEXT-FIG. 5. Lateral increase in *Thysanophyllum orientale* Thomson, topotype, UQ F46767. Numbers below figures are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum; A = alar septum. 1*a-j*, typical hystero-ontogenetic sequence; *a-c*, initial stage of development, showing formation of five parent septa (*b*) and subsequent formation of the dividing wall (*c-d*); *d-e*, hystero-brephic stage; *f-j*, early neanic stage, $\times 4$. 2*a-e*, non-typical hystero-ontogenetic sequence in which the dividing wall is formed independently of septa and the parent corallite becomes incorporated into an adjacent adult corallite. Note that lonsdaleoid dissepiments are present at the beginning of development of the daughter corallite (*a-c*) and these subsequently become modified to interseptal dissepiments (*d-e*), $\times 4$. 3*a-e*, variation in the length of axial septa distally in an adult corallite and development of two daughter corallites, $\times 2$.

are positioned nearest the counter septum, but in RSM 1966.6.4 they are nearer the cardinal septum.

Early neanic stage (text-fig. 5, 1*f-j*). Insertion during this stage of development is not always confined to the fossulae and is quite variable, with groups of septa seeming to appear almost simultaneously. Minor septa, along with the first dissepiments, are formed in all quadrants at the same time as the major septa. Dissepiments during this stage of development are interseptal in nature, and about two or three rows are formed. Occasionally a few lonsdaleoid dissepiments are also present in parts of some corallites.

Late neanic stage (lower daughter corallite of text-fig. 5, 3*d*). The start of this stage is taken at the appearance of a lonsdaleoid dissepimentarium by the retreat of septa from the wall. The lonsdaleoid area of UQ F46767 is variably developed and some corallites may reach adult proportions and still lack a zone of these dissepiments around the corallite. Minor septa either disappear or become very short with the formation of the lonsdaleoid dissepiments.

A long cardinal septum and short counter septum are present in some adult corallites of UQ F46767 (figs. 3*a-e*). Tracing these septa distally has shown that their length is quite variable, but shortening of the counter septum is more persistent than lengthening of the cardinal septum. The cardinal septum at its greatest length extends to the axis or slightly across it (fig. 3*c*), and when it is shortened, it may dissociate from its axial end leaving a thin axial structure (figs. 3*d-e*). During further corallite growth, this axial structure slowly decreases in length and eventually disappears.

One unusual example of increase was observed in UQ F46767 (text-fig. 5, 2*a-e*), in which the daughter corallite arises in an aseptate parent and the dividing wall is formed without the usual association of parent septa. As this wall develops, the wall separating the parent corallite from an adjacent adult corallite is progressively shortened and the area formerly occupied by the parent becomes incorporated into this adjacent corallite.

COMPARISON OF CHARACTERS OF INCREASE

Significant differences in the hystero-ontogenies of *Lonsdaleia* and *Lithostrotion* (see Jull 1965) are as follows: (1) more corallites may develop simultaneously from the same parent in *Lonsdaleia* than is known in *Lithostrotion*; (2) the daughter and parent corallites of both cerioid and fasciculate species of *Lonsdaleia* are separated by a dividing wall, whereas in fasciculate forms of *Lithostrotion* a partition usually separates daughter from parent corallite; (3) *Lonsdaleia* has zaphrentid insertion in all quadrants during early development and a prominently long cardinal septum; (4) tangential orientation of daughter to parent occurs in some corallites of *Lonsdaleia* but is unknown in lateral increase in *Lithostrotion*; (5) the axial structure in *Lonsdaleia* is initiated by the axial end of the cardinal septum forming the median lamella, whereas in *Lithostrotion* the columella is usually formed by dilation at the axis of the united axial septa.

A comparison of the hystero-ontogeny of *Thysanophyllum orientale* with that in the above genera shows that this species is not closely allied to either genus. Some characters, however, suggest that it lies with the Lonsdaleiidae. The cardinal septum during early development resembles that in *Lonsdaleia* and the manner of formation of dissepiments

is fundamentally similar in both forms although they tend to appear later during development in *T. orientale*. Moreover, the axial structure in parts of some corallites of the topotype studied and of the specimen from Bathgate, West Lothian, which was figured by Hill (1940, pl. 8, fig. 31) is similar to that in diphymorphic corallites of *Lonsdaleia* (see Pl. 100, fig. 1). One character which might suggest affinities between *T. orientale* and the Lithostrotionidae is the mesa-shaped tabulae in the species, a character sometimes present in *Lithostrotion* but unknown in *Lonsdaleia*. Strikingly different from both *Lonsdaleia* and *Lithostrotion* is the irregular pattern of septal insertion and the appearance of minor septa in all quadrants at or near the start of insertion in *T. orientale*.

Unlike *Thysanophyllum minus* Thomson, which is most likely a diphymorph of *Lonsdaleia floriformis floriformis*, *T. orientale* is obviously not closely allied to *Lonsdaleia* but possibly shares a common ancestor with this genus. Smith (1916, p. 235) agreed with the suggestion of Carruthers (*in* Garwood 1913, p. 563) that the Lower Viséan C_1 to C_2S_1 *T. pseudovermiculare* McCoy is ancestral to *Lonsdaleia*. Perhaps it also gave rise to *T. orientale*. The horizon of the *T. pseudovermiculare* beds in the North-West Province is now considered to be wholly within the basal Viséan Upper Caninia (C_2S_1) Zone (see Turner 1950, pp. 125, 128–9; 1959, p. 259).

In conclusion, *Thysanophyllum*, as presently interpreted, is undoubtedly a polyphyletic genus with some species related to the Lithostrotionidae. However, the family affinities of the genus must nevertheless lie with its type species, a probable lonsdaleoid, and species with different affinities can only be regarded as homeomorphs.

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THE 'DWARF' CROCODILES OF THE PURBECK FORMATION, DORSET: A REAPPRAISAL

by JOYCE JOFFE

ABSTRACT. *Nannosuchus gracilidens* and *Theriosuchus pusillus* were described by Owen, who believed that they were dwarf goniopholid crocodiles, adapted for preying on the contemporary small mammals. Several skull characters, which are now known to alter during life in modern crocodiles, were investigated in these 'dwarfs'. A number of these characters in *Nannosuchus* indicate that it is merely a juvenile form. Furthermore, since a larger form from the same beds, *Goniopholis sinus*, exhibits several specific features found also in *Nannosuchus*, it is concluded that the latter is the juvenile of *G. sinus*. Both the skull morphology of *Theriosuchus* and the presence of similar, larger remains in the same bed, indicate that it, too, is a juvenile. Reappraisal of its characters shows that it belongs to the family Atoposauridae and not to the Goniopholidae. The goniopholids have been suggested as possible ancestors of the later, eusuchian crocodiles. However, signs of progression towards eusuchian characters are unknown in the goniopholids, but are found in such atoposaurids as *Theriosuchus* and a recently discovered form from Texas. The Atoposauridae therefore appear to merit investigation as possible ancestors of the Eusuchia. The meaning and usage of the term 'dwarf' are briefly discussed.

THE Mesosuchia, predecessors of modern crocodiles which inhabited the oceans and river complexes of late Jurassic times, are not uncommon as fossils. By this period they were already differentiated into long-snouted and short-snouted varieties, and all forms variously possessed most of the typical crocodilian characters such as:

1. A false palate formed by the premaxillae, maxillae, and palatines.
2. A pes modified to allow movement between the tarsals.
3. An armour of dermal osteoscutes.
4. A 'cranial table'.
5. A pubis totally excluded from the acetabulum.
6. Amphicoelous or amphiplatyan vertebrae.

They were distinguished from their Tertiary descendants, the Eusuchia, in that these more advanced forms had incorporated the pterygoids into their false palate, and had evolved procoelous vertebrae.

Members of one particularly widespread family of mesosuchians, the Goniopholidae, are the subject of this paper. In particular, the species *Nannosuchus gracilidens* and *Theriosuchus pusillus* will be discussed. These were originally discovered and collected from the freshwater limestones of the Purbeck Series of Dorsetshire (south-west England) by William Husband Beckles Esq., and later described and figured by Sir Richard Owen (1879a).

The outstanding feature of these two crocodiles is their extremely small size, which Owen interpreted as 'dwarfism'; the evidence for this view will be examined critically. This examination leads to a reappraisal of Owen's assignment of both the genera to the Goniopholidae; an attempt has also been made to reconstruct something of the environment and habits of these crocodiles, and to discuss them in the context of the evolution of the Eusuchia as a whole.

STRATIGRAPHY AND PALAEOECOLOGY

In late Jurassic times the 'Purbeck Basin' lay just to the west of the 'Wealden Basin' and the two formations represent a continuous depositional series in a slowly changing environment. Nevertheless, detailed study has been almost confined to the succeeding Wealden formation.

It is clear from the work of Taylor (1963), Casey (1963), and Allen (1959) that the area had been covered for some time by a sea which extended over southern England and most of France, and analysis of the ostracod fauna shows that by Purbeck times this sea had receded, leaving behind brackish and, finally, freshwater conditions. Casey shows that a large land mass was present to the north, spanning an area roughly from London to Belgium. Rivers draining this land mass formed a low-lying deltaic swamp (probably similar to present-day mangrove swamps) with alternating euryhaline and freshwater faunas. The sea made only a few temporary incursions into this lagoonal complex. One of these, however, was very widespread and caused the breakdown of the northern land barrier. This marine invasion is represented by an oyster bank, the so-called 'Cinder Bed', so extensive and so easily traceable that Casey has suggested using it as a marker horizon for the boundary of the Jurassic and Lower Cretaceous. His suggestion has been adopted by the British Mesozoic Committee, and the Lower Cretaceous is now regarded as beginning immediately above the Cinder Bed.

About 10 ft. below the Cinder Bed, still well within the freshwater limestones and lacustrine shales of the typical Middle Purbeck sequence, lies the horizon in which the 'dwarf' crocodiles are found. The original locality is now within private grounds, and correlation of the sections worked out by early geologists in the area (Austen 1852, Damon 1884) with the present exposure on Durlston Head is very difficult as the actual bed is mentioned by name (the 'Feather Bed') only in these sections. Comments on the lithology of this bed will therefore be confined to the blocks containing the fossil material.

The 'Feather Bed' is a fine-grained, pale grey, bioclastic limestone composed of débris (largely of gastropods) and an almost pure calcareous matrix. The argillaceous content is small and there are a few fragmentary plant remains. It is fairly finely bedded and there are traces of lamination within each bed. This type of bed appears to fall into Taylor's (1963) category of 'on delta' deposits, in which sedimentation is said to be extremely slow.

On the upper bedding planes the vertebrate material is undistorted and only slightly crushed, but between these planes is a 'bone soup' of crushed and distorted remains, disarticulated and, for the most part, unrecognizable. There is practically no interstitial matrix. Between bone layers the limestone is a calcareous ooze, and it seems likely that the 'Feather Bed' may represent an area where material dropped out of suspension and accumulated slowly on the delta floor, having been brought there by one or many rivers.

Materials. The two crocodilian species with which this paper is concerned are *Nannosuchus gracilidens* Owen and *Theriosuchus pusillus* Owen. All the material is in the Department of Palaeontology, British Museum (Natural History).

The remains of *Nannosuchus* consist of one fairly complete skull showing dorsal view only (the holotype—No. 48217), several incomplete lower jaws with teeth (Nos. 48244, 48329, 48217, and 48328), some isolated dermal scutes and other post-cranial remains in rather poor condition.

The remains of *Theriosuchus* include one well-preserved, fairly complete skull (the holotype—No. 48330), somewhat crushed but still three-dimensional with a partly exposed palate and a firmly attached lower jaw; a partially articulated skeleton (No. 48216); several blocks containing fragmentary or crushed material (Nos. 48273 and 48260); several incomplete lower jaws (Nos. 48240 *a* and *b*, 48302 and 48260); and an isolated femur (No. 48333). Material from the British Museum (Natural History) collection of Recent *Crocodylus spp.* was used for comparison.

Methods. Preparation in acetic acid was attempted and found to be unsuitable for two reasons. First, the material below the bedding plane, when exposed by this method, was found to be too crushed to be of value. Second, even the exposed material was found to be riddled with minute fractures and microcracks which were not apparent until the block was developed and the material isolated. It was not possible to prepare the material mechanically as the skulls and skeletons are important typespecimens which have been figured.

THE 'DWARF' CROCODILES

The new small crocodiles from the Purbeck beds were discussed by Owen in two papers published in 1879. In one (1879*a*) the morphology of both genera is given in some detail, and this is followed by a section in which their ecological relationships to the contemporary small mammals are discussed. In the other paper *Theriosuchus* alone is described; this is followed by an almost identical discussion of its ecology.

In these papers, Owen's main reason for regarding these genera as dwarf forms is that, in both genera, the specimens are all of uniformly small size, suggesting that this was the final, adult size. He then points out that these small crocodiles were contemporary with the small Mesozoic mammals, and suggests that the crocodiles may be dwarf forms which have become reduced in size, or dwarfed, in order to adapt to the size of this prey.

It is convenient to discuss first this ecological aspect of Owen's argument. It is certainly true that mammals do occur as an element in the varied vertebrate and invertebrate faunas of this horizon (Damon 1884). But, while Owen's suggestion may be correct, it is important to realize that, owing to the nature of the delta deposits, the fauna could well be a death assemblage, its members never being associated during life. Added to this, the work by Cott (1961) on *Crocodylus niloticus* indicates that young crocodiles feed upon invertebrates and fish, and prey upon mammals only later in life. This fact may be relevant to the possible feeding habits of the small fossil forms, whether or not these were dwarfs.

One of Owen's original reasons for believing that the two genera were dwarf forms was, as noted above, his assumption that the genera were of constant, small size. The validity of this assumption was first checked by taking measurements of a number of lower jaws (see Table 1). Where these were incomplete, the estimated original length is inserted in brackets.

From these series it may be seen that the sizes range from 4 cm. to 17 cm. in *Nannosuchus* and from 3.5 to 10.4 cm. in *Theriosuchus*. It is clear that Owen's belief that the specimens were of constant size is unfounded; there appear instead to be two growth series.

However, although the specimens are not of uniform size, even the largest is quite small and the genera may still be dwarf forms. It is therefore now necessary to attempt to establish whether these specimens show any specifically juvenile, or any specifically adult, features. Various characters of this kind may be found in Mook's (1921) work on

TABLE 1

Nannosuchus

<i>Specimen No.</i>	<i>Incomplete jaw length (cm.)</i>	<i>Estimated complete length (cm.)</i>
48328	2.5	(4.0)
48244	8.0	(9.5)
48329	8.5	(9.5)
48217 (type)	12.0	
48217 (different individual)	12.0	(17.0)

Theriosuchus

48240 (<i>a, b</i>)	2.8	(3.5)
48260	6.5	(7.5)
48330 (holotype)	7.2	(8.4)
48302	10.4	

individual and age variations in Recent crocodiles. A study of both Recent and fossil material in the British Museum (Natural History) both verified and amplified Mook's work. Six main characters were investigated, as follows:

1. *Skull ossification and rugosity.* Mook's growth series of Recent crocodiles showed, not surprisingly, that the degree of ossification and rugosity increased with age. In particular, the margins of the cranial table and orbits became overgrown in the older specimens.

2. *Development of the cranial table.* This second criterion taken from Mook's work was found to be of limited use, as the cranial table develops so soon after hatching that it is helpful in identifying only extremely young individuals.

3. *Closure of the sutures.* From examination of the growth series from the British Museum's collection, it was apparent that the sutures on the dorsal surface of the skulls became increasingly obscured in older specimens. In contrast, the palatal sutures remained clearly visible, and these therefore provided a less useful guide than the dorsal sutures.

4. *Size and shape of the supratemporal fenestrae.* The supratemporal fenestrae in crocodiles were found, as Mook discusses, to be slit-like in very young animals; they tended to widen out during ontogeny until at maturity they were roughly circular in shape. Young individuals also tended to have large orbits, and the size of the fenestrae relative to the size of the orbits changed throughout youth. In caimans, however, the supratemporal fenestrae were found to have a tendency to become smaller and sometimes to close up completely in old age.

5. *Ratio of pre-orbital to post-orbital length of the skull.* The changes in this ratio for *Crocodylus americanus* are shown in Table 2, taken from Mook's paper. Other comparative material studied gave similar results, though the growth series was not adequate for as complete a table of measurements as that below. It is clear that the snout tended to become relatively longer (compared with the post-orbital region) during life.

6. *Robustness of the teeth.* In all growth series observed, both by Mook and the

author, the teeth increased in girth with age and provided a general clue to the age of an individual.

TABLE 2

	(a) Length of post-orbital region (cm.)	(b) Length of pre-orbital region (cm.)	Ratio a/b
<i>Crocodylus americanus</i>			
Mus. Comp. Zool. No. 5002	3.0	3.3	0.909
Mus. Comp. Zool. No. 5008	3.7	5.2	0.711
Mus. Comp. Zool. No. 5007	4.5	7.0	0.642
Amer. Mus. No. 15182	6.5	12.6	0.515
Mus. Comp. Zool. No. 5032	7.2	14.8	0.486
Amer. Mus. No. 15175	9.7	20.8	0.466
Amer. Mus. No. 7120	11.8	26.0	0.453
Amer. Mus. No. 7132	12.0	27.8	0.431
Amer. Mus. No. 7121	12.2	28.1	0.433
Mus. Comp. Zool. No. 5391	12.5 (est.)	33.0	0.378
Mus. Comp. Zool. No. 10921	16.5	33.0	0.500
Mus. Comp. Zool. No. 13904	15.5	41.5 (est.)	0.373
Amer. Mus. No. 7139	17.0	53.0	0.320

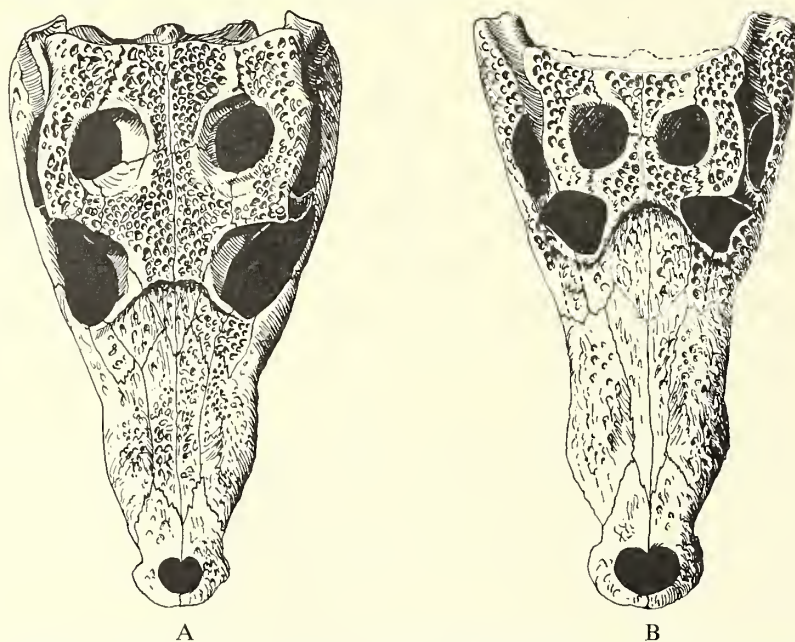
The condition of *Nannosuchus gracilidens* (text fig. 1a) with respect to the above criteria is as follows:

1. The skull is lightly ossified.
2. The cranial table is present but unthickened.
3. The sutures on the dorsal surface are relatively unobscured.
4. The supratemporal fenestrae do not possess that degree of rounding noted in mature Recent forms, and the orbits are relatively large.
5. Since only a single skull is known, its relatively short snout could be interpreted either as the juvenile stage of a long-snouted form, or as the adult of a short-snouted form. This character is therefore inconclusive.
6. The teeth of *Nannosuchus*, which are unfortunately disarticulated from the skull, are extremely slender and sharply recurved.

This evidence, which suggests that the skull of *Nannosuchus* is of a juvenile form, is not conclusive. Conclusive identification of *Nannosuchus* as a juvenile would require the discovery of a form whose morphology was in general similar to that of *Nannosuchus*, but which had such adult features as an increased degree of ossification, especially in the cranial table, less clear sutures on the dorsal surface, a more circular supratemporal fenestra, relatively smaller orbits and longer snout, and larger, more robust, teeth. Search for such a specimen revealed, among the larger Purbeckian gonio- pholids, the skull of *Goniopholis simus* (text fig. 1b) from the same horizon as *Nannosuchus*, and which was also originally described by Owen (1878). Owen's reasons for separating *Nannosuchus* from *Goniopholis* were its smaller size and more slender teeth—features which, on the basis of the above survey, cannot be regarded as taxonomically reliable. Furthermore, *Goniopholis* is extremely similar to *Nannosuchus* in details of the skull dermal bone-pattern, in the shape of the external naris and in the shape of the cranial table. Also, both genera possess an identical shallow curved ridge on the frontals,

continuous with the anterior margin of the orbit; this feature was noted by Owen and termed the 'semi-lunar ridge'. Finally, the differences between the two forms are, both in nature and in degree, readily explicable as being due to growth changes, as follows:

1. The supratemporal fenestrae of *Goniopholis simus* have the typical circular outline of a mature individual.
2. The orbits are relatively smaller in *Goniopholis simus*.
3. *Nannosuchus* has a ratio of pre-orbital to post-orbital length of 1:1. This ratio in *Goniopholis simus* is 2:1. This greater proportional snout length in the larger specimen shows clearly in text fig. 1 (*a* and *b*).



TEXT-FIG. 1. Dorsal views of the skulls of A, *Nannosuchus gracilidens* (type specimen, BM(NH) No. 48217) $\times \frac{2}{3}$; B, *Goniopholis simus* (type specimen, BM(NH) No.41098) $\times \frac{1}{5}$.

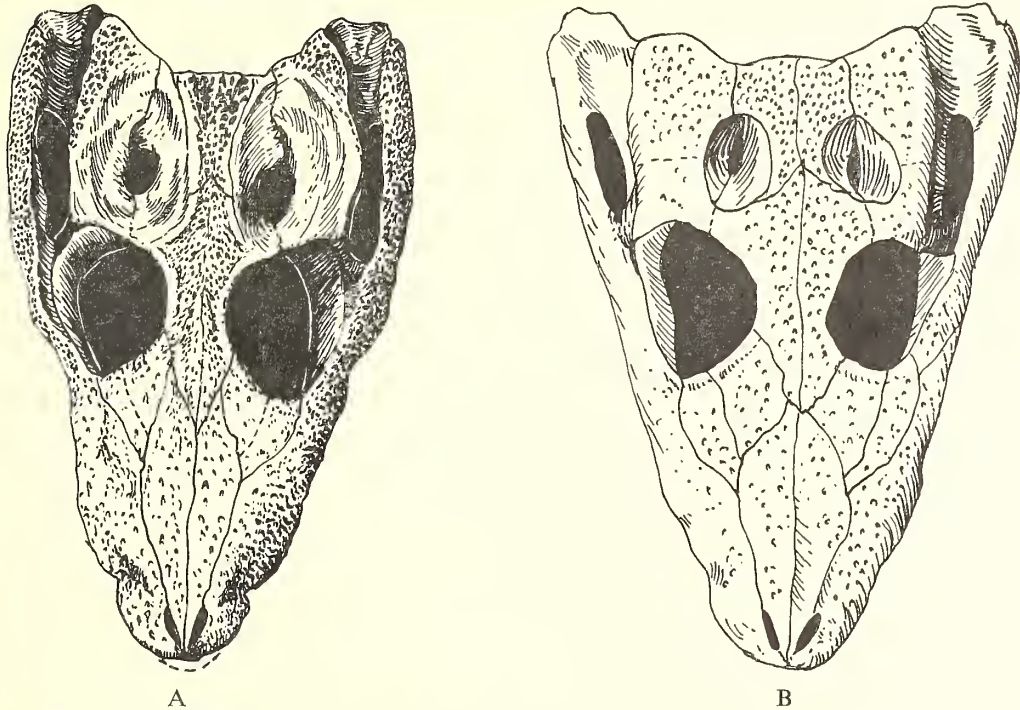
These characters strongly suggest that *Nannosuchus* is merely a juvenile *Goniopholis*. The great similarity between *Goniopholis simus* and *Nannosuchus gracilidens* indicates that the two species are closely related. There are, however, certain differences. First, the teeth of *Nannosuchus gracilidens* are so much more slender than those of the type skull of *Goniopholis simus* that the differences might conceivably be adaptive and not merely due to an age difference. Second, the pitting and ornament on the skull roof of *Nannosuchus* appears to be denser than in *G. simus*. This could represent a specific difference between them, but might also be due to weathering and a difference in preservation.

It is clear that there is just enough difference between these two forms for it to be possible to separate them into two species; this is the 'knife-edge' of taxonomy. However, as the two forms are known from the same series and locality it is preferable to regard them as conspecific, in the absence of any compelling reason for doing otherwise. *Nannosuchus*

gracilidens Owen may therefore be regarded as a junior synonym of *Goniopholis simus* Owen.

Theriosuchus pusillus (Fig. 2a) may now be examined similarly to establish its condition with respect to the criteria of age which were listed above:

1. The ossification of the skull is very slight.
2. The cranial table is unthickened.
3. The sutures are visible (though somewhat obscured by crushing).
4. The supratemporal fenestrae are not rounded, but are small and slit-like, and the relative size of the orbits is extremely large.



TEXT-FIG. 2. Dorsal views of the skulls of A, *Theriosuchus pusillus* (type specimen, BM(NH) No. 48330), natural size; B, the atoposaur *Alligatorium meyeri*, natural size (after Lortet).

These criteria suggest that the type of *Theriosuchus* is an immature individual, and the presence of a femur assigned to the same genus (and indeed very similar to other femora of *Theriosuchus*), but almost twice the size of those on the block containing post-cranial remains (No. 48216), reinforces this view.

The affinities of this crocodile present greater problems than those of *Nannosuchus*. *Theriosuchus* is quite unlike typical goniopholid in the following characters:

1. The skull is extremely short-snouted, shorter even than that of a young goniopholid.
2. The orbits are far larger than the supratemporal fenestrae. Their size exceeds the estimated proportion in a young goniopholid of the same size.

3. The nasals bisect the external naris leaving paired apertures, a feature otherwise unknown in the Goniophoridae.
4. The areas occupied in *Theriosuchus* by the supratemporal fenestrae are covered with smooth thin bone, lappets of which close the fenestrae almost entirely, leaving only small slits. This overgrowth is not observed in any other goniopholid.
5. Very large palpebral bones are present, the ornament and pitting of which are similar to that of the skull. Palpebrals have not been described from any of the other known specimens of goniopholid, though this could be an accident of preservation.
6. The teeth are blunt, rounded, and spatulate, not conical or sharp as in other goniopholids.
7. The scutes are small and square, and show no sign of the characteristic goniopholid peg-and-socket articulation.

This last feature was one of the chief criteria used by Owen in assigning *Theriosuchus* to the family Goniophoridae. He figures one scute in his monograph, and shows the supposed peg, but this scute cannot be found among any of the material in the *Theriosuchus* collection. Since none of the scutes so far examined shows any sign of either peg or socket, it must be assumed that the feature noted by Owen was an artefact of preservation.

While the small size of the skull, plus many of the features outlined above suggest that the type specimen is that of a juvenile, like *Nannosuchus*, there is no similar but larger form known from any British horizon. However, crocodiles are also known from the Kimmeridgian of the Rhône area (i.e. from beds slightly older than those containing *Theriosuchus*). These forms have been described briefly by von Meyer (1851) and more thoroughly by Lortet (1892), and have been placed in a distinct family, the Atoposauridae. *Theriosuchus* and the atoposaurids are closely similar in many respects, as follows (see Fig. 2):

1. They are all small forms, the largest known being less than 90 cm. long.
2. They are all very short-snouted.
3. The orbits of all are proportionally large compared with the supra-temporal fenestrae.
4. The naris is paired in some genera of atoposaurids, as in *Theriosuchus*.
5. In all genera the supratemporal fenestrae are more or less overgrown—in one genus (*Alligatorellus*) they are entirely imperforate.
6. In all atoposaurids figured, the teeth appear blunt and rounded, as in *Theriosuchus*.
7. The osteoscutes are also similar in the two groups, being square and small with median longitudinal ridges on the dorsal scutes and shallow 'pinhole' pitting.

Even though the other post-cranial elements are not available for comparison, there can be little doubt that *Theriosuchus* is an atoposaurid. The appearance of an atoposaurid in England is not surprising, since both south-east England and the Rhône area were part of the same fluctuating basin. It is therefore proposed to transfer *Theriosuchus pusillus* Owen from the family Goniophoridae to the family Atoposauridae.

NOTE ON THE PROBLEMS OF EUSUCHIAN ANCESTRY

Cainozoic crocodilians, including the extant and almost all the extinct forms, are grouped together in the sub-order Eusuchia, the chief characters of which are as follows:

1. The vertebrae are procoelous, not amphicoelous or amphiplatyan as in the mesosuchians.
2. The pterygoids have entered into the formation of the secondary palate, whereas in the mesosuchians this is composed only of premaxillae, maxillae, and palatines.
3. The internal openings of the eustachian canal are enclosed in bone.
4. The external naris is undivided.
5. The supratemporal fenestrae tend to be small.
6. The post-orbital bars have become subdermal.
7. The frontals do not usually enter into the margins of the supratemporal fenestrae.

Characters 1, 2, and 3 are critical and definitive for the sub-order, while 4-7 are variable and are also possessed in 'mosaic fashion' by many mesosuchians.

Since all the Cainozoic Eusuchia are fully eusuchian in their characteristics, the group must have evolved from some progressive mesosuchian group (or groups) in the late Mesozoic. Romer (1956) has suggested that they may have evolved from the goniopholid mesosuchians. This family was common and widespread in the Cretaceous and possessed several generalized features (e.g. dermal bone pattern on the skull, sunken postorbital bar, undivided external naris) which would not debar them from ancestry of the Eusuchia. However, as far as is known, they all have amphicoelous vertebrae, and even the latest members have a typically mesosuchian palatal structure.

The goniopholids do not appear, in these two features at least, to be progressing towards the eusuchian conditions. It is therefore interesting to find that two genera of another mesosuchian family, the Atoposauridae, were more progressive in these features. The two genera are *Theriosuchus* and a small crocodilian recently found in the Wealden of Texas (i.e. slightly later in time than the Purbeckian) by Dr. Langston of the University Museum of Texas. The features of this new crocodile, as described by Dr. Langston (*personal communication*) seem clearly to ally it with *Theriosuchus* in the Atoposauridae. It has a similar short snout and very large orbits, a similar naris, similar blunt rounded teeth, and similar palpebral bones, while the pattern of dermal bones, and their ornament, are also similar to those of *Theriosuchus*. Dr. Langston has also found procoelous vertebrae in his specimen, and it is interesting to note that, in the specimen of *Theriosuchus* which shows the post-cranial skeleton (No. 48216), a single vertebra which is probably an anterior caudal has been displaced so that the face of the centrum can be seen. This is clearly procoelous, but has a central depression which is also found in the Texas specimen. It is quite unlike the typical amphicoelous centra of other mesosuchians, though its degree of convexity is not as great as in later eusuchians. *Theriosuchus* is therefore the earliest known procoelous crocodile.

Significantly, the condition of the palate is different in the Purbeck and Texas forms. In *Theriosuchus* the internal nares continue posteriorly into a median depression, extending beneath the pterygoid region. This depression (which may have been covered below by a soft palate in life) is walled laterally by outgrowths of the pterygoids, and roofed by the palatines. This condition is more advanced towards the eusuchian palatal

structure than is that of the typical mesosuchians. The American specimen is further advanced: the internal naris has migrated posteriorly and the pterygoid flanges are more extensive than those of *Theriosuchus*, though they do not meet in the midline, nor do they extend beneath the median depression ventrally, as in eusuchians, to form a posterior elongation of the false palate.

While these atoposaurids are early enough to provide possible eusuchian ancestors, the members of the family so far discovered are perhaps too specialized in their small size, dentition, large orbits, and overgrown supratemporal fenestrae to be themselves wholly acceptable as such ancestors. If they do prove to be unrelated to the Eusuchia, the atoposaurids at least provide an interesting example of parallel evolution.

REMARKS ON THE CONCEPT OF DWARFISM

Dwarfism has two main connotations, the first of which may be dismissed for the purpose of this discussion, being a pathological term applied to individuals with specific genetic or physiological defects. The second meaning of the term is very widely used in biology to define small varieties of animal or plant closely related to other, larger varieties. It is possible to produce 'dwarf' varieties by controlled, selective breeding, and, of course, the same process can occur in nature. Far more commonly found in nature, however, is the opposite tendency, namely the tendency to grow larger, the reasons for which need not be discussed here. But to use the term 'dwarf' to describe an individual or species whose evolutionary history is unknown is to render meaningless the essence of the term 'dwarfism', inherent in which is the process of reduction from a previous larger size. Thus a small creature is not a dwarf *sensu stricto* unless it has evolved from a larger ancestor. When limited in this way, the definition naturally excludes most small members of the animal and plant kingdoms.

The suitability of the term 'dwarf' to describe Owen's small genera may finally be considered briefly. *Nannosuchus* is, of course, no longer a problem; as discussed previously, it is merely a juvenile. The position of *Theriosuchus*, however, has not been defined above. One may first note that the material of *Theriosuchus* belongs mainly to immature individuals (the isolated femur being perhaps an indication of the possible size of the adult). No known atoposaurid is longer than 90 cm., however, the American specimens (very probably members of the same family) being likewise of small individuals. There is no evidence that any larger atoposaurids or atoposaurid ancestor ever existed. The reasons for this small size are probably various; for example, it may be a result of the absence of larger predators, or of the presence of a supply of small food, etc. However, Owen's belief that they had actually reduced their size has no foundation on present evidence. It is therefore suggested that the 'stigma' of dwarfism should be removed from them and that they should henceforth be recognized for what they are, a group of small and extremely interesting mesosuchian crocodiles.

SUMMARY AND CONCLUSIONS

The purpose of this paper has been to re-examine Owen's so-called 'dwarf' crocodiles of the Purbecks. On detailed reinvestigation it was realized that the first of the two species, *Nannosuchus gracilidens*, was based on an immature individual of *Goniopholis*

simus from the same horizon and locality. The second species, *Theriosuchus pusillus*, which was originally assigned to the family Goniopholidae, was removed from this family and placed in the Atoposauridae, a family of advanced and specialized mesosuchians, known hitherto only from the Kimmeridgian of the Rhône area and Bavaria. One of the interesting features of the atoposaurids is that they do indeed appear to have been all small forms; though, in the author's opinion, the term 'dwarf' cannot be applied to them in the strict sense, there being no evidence of size reduction from a larger ancestor. The advanced features of the family Atoposauridae include a palate more eusuchian than that of typical mesosuchians, and the earliest record of a procoelous vertebra in the Crocodilia. They are, however, too specialized to have been direct eusuchian ancestors, and must therefore be included among the several Upper Mesozoic mesosuchians which paralleled those features which later became characteristic of the successful Eusuchia.

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BRAZILIAN PALAEOZOIC ALGOMYCETES AND TASMANACEAE

by FRIEDRICH W. SOMMER *and* NORMA M. VAN BOEKEL

ABSTRACT. Synopsis of nature and distribution of Devonian marine plant microfossils from Brazil.

This paper comments on a series of plant microfossils found in Devonian marine strata in Brazil, which for various reasons have not received the attention and interest they deserve. Some of them have been known for a long time but the communications concerned did not catch the eye of modern palaeobotanists of the Northern Hemisphere. More recently there has been a language barrier, because papers on present-day Brazilian palaeobotanical research have been published in Portuguese. On the other hand Brazilian fossils, when mentioned, have not always been compared with the necessary accuracy, in part due to the geographical separation, but also because the early material has been lying eighty or more years in American and European institutions. Thus we offer the following synopsis because references to Brazilian plant fossils do not always correspond with more recent research results.

Class ALGOMYCETES Kräusel 1941

Description. Thallophytes provided with pseudotissue (Scheingewebe) similar to mycelia of fungi; they possess simultaneously characters of fungi and algae, without fitting into either group.

Order PROTOSALVINIALES Sommer 1962

(Foerstiales Kräusel 1941)

Description. With the characters of the class and spore tetrads present.

Family PROTOSALVINIACEAE Sommer 1962

(Foerstiaceae Kräusel 1941)

Description. Spore tetrads present within the thallus.

Genus PROTOSALVINIA Dawson 1884 emend. Sommer and van Boekel 1966

Type species. *Protosalvinia braziliensis* Dawson 1884.

Description. Thalloid bodies provided with tetrads of spores which may be visible or not; waxy covering present or not; variable in size and form, the surface may imitate a polygonal cellular pattern.

Key. A. Thalloid bodies with spore cavities clustered in the upper part; these are situated in subsurface depressions, the tetrads are visible without any laboratory treatment, and the walls are not covered with waxy material; spore cavities may be hidden under a 'lid' which falls easily out without applying any special device.

- a. Not lobed or divided; thalloid bodies 'sessile', spherical to oval or reniform:

Protosalvinia braziliensis Dawson 1884

Occurrence. Middle Devonian, Curuá group; Amazon basin, Brazil.

- b. With two or more prominences (lobes); body more or less oval, reniform, 'sessile' to stalked:

Protosalvinia bilobata Dawson 1884 emend. Sommer 1962

Occurrence. Middle Devonian, Curuá group; Amazon basin, Brazil.

For the sake of comparison we present the North American representatives of the genus as they are known to us from literature:

- B. Thalloid bodies which do not show tetrads and spore cavities without aid by laboratory treatment; waxy covering present.

- a. Thalloid bodies with apical lobes surrounding the cluster of spore cavities (visible after laboratory treatment):

Protosalvinia ravenna (White and Stadnichenko 1923) Arnold 1954

- b. Thalloid bodies stalked, bilobed; spore cavities mostly in one row beneath apical groove (visible after laboratory treatment):

Protosalvinia furcata (Dawson 1888) Arnold 1954

- c. Thalloid bodies stalked, with swollen head, spore cavity usually single with one spore tetrad lying at the bottom of funnel-like depression at the apex of the head:

Protosalvinia arnoldii Bhāradwaj and Venkatachala 1960

Order SPONGIOPHYTALES Sommer 1959

Description. Algomycete Thallophytes the tubiform stalks of which consist of a 'derm' of pseudoparenchymatous character and which, under examination, do not reveal the presence of chitin and the existence of spores.

Family SPONGIOPHYTACEAE Kräusel 1954

Description. Thallus simple, provided with lobes or branched dichotomously; external part of derm cellular, inner part of a 'tissue' similar to spongy hyphae.

Genus SPONGIOPHYTON Kräusel 1954

Description. Thallus simple, lobed, or dichotomized. Fundamental substance consisting of a tissue similar to branched hyphae of porous spongy aspect, provided with an outer layer of cellular aspect, where there are dark inclusions in form of buds, filling out small round spaces; besides these there are found larger elements, also dark of colour, composed of tissue which, when dissolved, leave holes of various forms and sizes.

Type species. *Spongiophyton lenticulare* (Barbosa 1949) Kräusel 1954.

Spongiophyton lenticulare (Barbosa) Kräusel 1954

1949 *Haplostigma lenticularis* Barbosa.

Description. Thallus (or parts of thallus?) with parallel margins, up to 7 mm. wide, sometimes wider, usually unbranched; a pedate surface of fixation; a 'parenchymatous' tissue of porous spongy character, with numerous longitudinal thicker trabeculae irregularly arranged, holes varying from slits to lenticular openings, directed longitudinally, 0.4–0.8 mm. long, in very variable number, irregularly distributed. Surface 'cells' elongated longitudinally.

Occurrence. Lower Devonian, Upper Ponta Grossa beds; State of Paraná, Brazil.

Spongiophyton namum Kräusel 1954

Description. Thallus more or less dichotomous, the branches generally 1–2.5 mm. broad (rarely broader), the top ends occasionally elliptically rounded, constricted. Inner constitution as in type species but thickened lines less numerous, the holes more or less circular to elliptic, diameter mostly 150–250 μ , rarely 340 μ , surface 'cells' polygonally foveolate.

Occurrence. Lower Devonian, Upper Ponta Grossa beds; State of Paraná, Brazil.

Spongiophyton minutissimum Kräusel 1954

Description. Thallus small, only a few mm. in length, dichotomously lobed, margins strongly thickened. Inner constitution as in *S. namum*, the numerous holes small, like needle punctures, with diameter generally 60–100 μ , rarely 150 μ , frequently transversally broadened. Surface 'cells' polygonally foveolate.

Occurrence. Lower Devonian, Upper Ponta Grossa beds; State of Paraná, Brazil.

Spongiophyton articulatum Kräusel 1954

Description. Thallus not completely known, 'parenchymatous' spongy tissue with numerous conspicuous thickened lines and many knob-like swellings, longitudinally corresponding on the outer derm with transverse creases.

Occurrence. Lower Devonian, Upper Ponta Grossa beds; State of Paraná, Brazil.

Spongiophyton hirsutum Kräusel 1954

Description. Thallus not completely known, 'parenchymatous' tissue spongy. Derm provided with appendages irregularly distributed, of variable length, beginning with broad base and ending in thorn or hair.

Occurrence. Lower Devonian, Upper Ponta Grossa beds; State of Paraná, Brazil.

Other records. To the knowledge of the authors of this paper, *Protosalvinia* has not been recorded in South America outside the Amazon sedimentary basin. *Spongiophyton*, in addition to its occurrence in the lower Devonian of Paraná, has so far been found in Devonian strata (*sensu lato*) of the states of Goiás, Piauí, and Maranhão. It seems that the Tocantins ridge somehow separated the two genera.

Outside Brazil and North America, *Spongiophyton* has been recognized by Kräusel (*personal communication*) among Chinese plant fossils, and *Spongiophyton lenticulare* is known from Russian Devonian strata (Textbook: Gothan and Weyland 1964, p. 70).

Class CHLOROPHYCEAE
Order TASMANALES Sommer 1960

Description. Globoid organisms which may be deformed in deposition; surface without appendages.

Family TASMANACEAE (Sommer) Sommer and van Boekel 1963

Description. Unicentric organisms, originally more or less spherical, generally compressed to a disc; haptotypic structures absent. Ornamentation mostly without high relief; where there is some sculpture, it is not exaggerated in detail or size as, for example, the spinae, clavae, capilli, etc., of spores or the multiform projections of the hystrichospheres. The Brazilian Tasmanaceae are divided into the two genera *Tasmanites* and *Tapajonites*.

Genus TASMANITES Newton 1875 emend. Schopf, Wilson, and Bentall 1944

Group 1. With conspicuous outer ring:

- Tasmanites roxoi* (Sommer 1953) Sommer and van Boekel 1965
- Tasmanites avelinoidi* (Sommer 1953) Sommer and van Boekel 1965
- Tasmanites lanegoi* Sommer 1956
- Tasmanites salustianoidi* (Sommer 1953) Sommer and van Boekel 1965

Group 2. With conspicuous punctae or pores, no outer ring:

- Tasmanites tapajonensis* (Sommer 1953) Sommer and van Boekel 1965
- Tasmanites harttii* (Sommer 1953) Sommer and van Boekel 1965
- Tasmanites derbyi* (Sommer 1953) Sommer and van Boekel 1965

Group 3. With conspicuous folds:

- Tasmanites mourae* (Sommer 1953) Sommer and van Boekel 1965
- Tasmanites erichsenii* Sommer and van Boekel 1963

Group 4. Oval to spindle-shaped:

- Tasmanites euzebioi* (Sommer 1953) Sommer and van Boekel 1965
- Tasmanites sommeri* van Boekel 1963

Genus TAPAJONITES Sommer and van Boekel 1963

Description. Unicentric discs, originally spherical, ranging approximately from less than 100 μ to more than 200 μ in diameter. Ornamentation consisting of rounded warts, lumps, or shields which extend beyond the outline of the disc or may be visible only when the specimen is manipulated under the low-power microscope and turned so as to 'stand' (in side view).

Distinction. *Tapajonites* is readily distinguished from *Tasmanites* by its relief and external ornamentation; wall about $\frac{1}{25}$ diameter, compact, not membranaceous.

Name derivation. After the Tapajós river, State of Pará, Brazil.

Type species. *Tapajonites roxoi* Sommer and van Boekel 1963.

Other species. *Tapajonites mosesii* (Sommer 1956) Sommer and van Boekel 1963.

REMARKS ON THE TASMANACEAE

The following comments on the Brazilian Tasmanaceae have been made by van Boekel (1966):

1. The same assemblages have been found in Devonian and Silurian strata of both banks of the Amazon river.

2. The species *Tasmanites salustianoi*, *T. sommeri*, and *T. erichsenii* are limited to the Amazon sedimentary basin.

3. *Tasmanites mourae* is ubiquitous in all Silurian and Devonian sedimentary basins so far investigated; this suggests a wide palaeogeographic distribution and vertical persistence.

4. Some of the species are reliable index-fossils for lower, middle, and upper Devonian strata; they do not occur in Carboniferous or younger strata in Brazil.

5. Of the five species described from the Tucano-Jatobá basin (state of Pernambuco), four (*Tasmanites lanegoi*, *T. mourae*, *T. tapajonensis*, and *Tapajonites mosesii*) were also found in the Devonian of Aragarças (state of Goiás).

6. A Devonian shale sample from eastern Bolivia (Sommer 1955, p. 183) provided an assemblage very similar to the one studied by the same author from a sample of Devonian shale from Jaguariaíva, state of Paraná.

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ADDENDUM

IN a recent paper, C. Downie (1967, *Rev. Paleobotan. Palynol.*, **1**, 279) registers *Tasmanites* as belonging to the Prasinophyceae.

THE DEVELOPMENT OF *GLOBIGERINOIDES RUBER* (D'ORBIGNY 1839) FROM THE MIOCENE TO RECENT

by W. G. CORDEY

ABSTRACT. Previous workers considered that *Globigerinoides ruber* d'Orbigny 1839 ranged, with no appreciable morphological change, from early Miocene (*Globigerinita dissimilis* zone) to Recent. The present study, based on material from various parts of the world, suggests that the early to Middle Miocene forms can be distinguished from the Uppermost Miocene to Recent forms on the basis of ontogeny and phylogeny. The early to Middle Miocene forms are referred to *Globigerinoides subquadratus* Bronnimann 1954, which is redefined, the younger forms (Uppermost Miocene to Recent) to *G. ruber*. The ancestral form of *G. subquadratus* was *G. quadrilobatus altiapertura* (Bolli 1957), and *G. subquadratus* s.s. (*G. ruber* of previous workers, e.g. Bolli 1957) first appears in the *stainforthi* and not in the *G. dissimilis* zone. Evidence from Jamaica suggests that a form broadly similar to *G. obliquus* Bolli 1957 is the ancestral form of *G. ruber* (here defined). An examination of the wall structure of the group reveals considerable variation, but there appears to be no fundamental differences between the earlier and later occurrences.

THIS study is an attempt to trace the development of *Globigerinoides ruber* d'Orbigny 1839, which first appears in widely separated areas at about the level of *Globigerinita dissimilis*, *G. stainforthi*, or *Globigerinatella insueta* zones and ranges through to Recent. There is a distinct break in the range of *ruber* in both the Caribbean area and in the East Indies (Bolli, *personal communication*), where it disappears at about the top of the *Globorotalia folisi robusta* zone (slightly higher in the East Indies) only to reappear at about the Uppermost Miocene or Basal Pliocene. It was suggested by J. B. Saunders (and partly by Dr. H. Bolli) that a comparative study of these two main occurrences might reveal differences between them which would be interesting, mainly from the phylogenetic point of view. There appeared to be no differences in external morphology between the two populations (cf. Bolli 1957, p. 114) and the investigation commenced with a study of the wall structure.

However the examination of over 100 thin sections from various levels failed to reveal any significant differences between the Miocene and younger material. Variations in wall structure were observed which compared with certain of the sections shown by Bé (1965) in the test of *Globigerinoides sacculifer* (Brady). It would appear that the wall structure of *G. ruber* could be affected by depth, as suggested by Bé (1965) in the case of *G. sacculifer* (and also *Globorotalia truncatulinoides* Bé 1963). Parker (1962) showed that thickening of the test can also be affected by changes in latitude.

However, in the process of thin-sectioning, differences were observed between the Miocene and younger forms and these are described in detail. For purposes of this discussion the Oligocene-Miocene boundary is taken at the base of the *Globigerina ampliapertura* zone (see Eames *et al.* 1962).

The material used in this study came from:

(a) The type localities of the *Globigerinita dissimilis*, *G. stainforthi*, *Globigerinatella*

insueta, and *Globorotalia fohsi robusta* zones of the Cipero Formation of Trinidad (collected by the author);

(b) Bodjonegoro No. 1, Java, ranging in age from *G. insueta* zone to the Pliocene.

(c) Jamaica, ranging in age from the *G. insueta* zone to the Pleistocene.

(d) A late Tertiary to Quaternary mid Pacific core CAP 38 BP.

In addition, two samples of late Pleistocene age from the Niger Delta, and also some Recent material, were examined.

The specimens are deposited at the British Museum (Natural History), whose registered numbers are quoted, prefixed BMNH.

SYSTEMATICS AND MORPHOLOGY

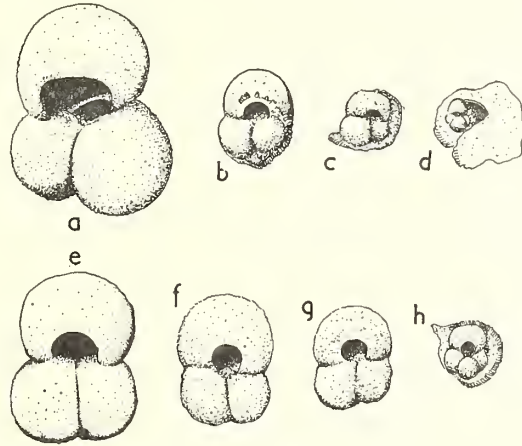
G. ruber is a very common and easily identified planktonic species. Fossil material was described by Bolli (1957) and Banner and Blow (1960), while the ecology and morphology of the living form was discussed in some detail by Bradshaw (1959), Bé (1959), Parker (1962), and Cifelli (1965). It is restricted in Recent seas to tropical and temperate waters. Banner and Blow (1960, p. 21), in their discussion of the species, considered that *Globigerinoides subquadratus* Bronnimann 1954 was at least subspecifically distinct. The writer regards Bronnimann's species as quite distinct from *G. ruber*, as discussed more fully below. The high spired forms encountered in this study differ from *Globigerina pyramidalis* (Van den Broeck 1876) with respect to the supplementary apertures. The type figure of *G. pyramidalis* shows two supplementary apertures on each chamber but they are not placed symmetrically over the dorsal intercameral sutures as in *G. ruber*.

Although variation in morphology is observed in *G. ruber*, the character which appears to vary least is the primary aperture. This is usually a broad arch placed symmetrically with respect to the penultimate and antepenultimate chamber suture. The shape of the aperture appears to be fairly constant (text-fig. 1). It is a useful character in distinguishing *G. ruber* s.l. from forms which bear a gross morphological similarity to it, e.g. *Globigerinoides elongatus* d'Orbigny 1826, which has a more consistently ovate primary aperture (Banner and Blow 1960, pl. 3, fig. 10c).

One considerable difficulty experienced was to determine the exact number of chambers in the tests of individuals at various stratigraphic levels; this is because of test thickening over the apical area, obscuring the detail of the initial whorl. In Pleistocene and Recent material it was possible to remove successively older chambers, and obtain an accurate count. The maximum number of chambers observed was twelve, excluding the proloculus. This differs somewhat from Parker's (1962) observations, which gave a maximum number of seventeen. Infilling of the chamber lumen, in the early to Middle Miocene material (*robusta* zone and older), prevented study by successive chamber removal. Particularly well-preserved material from the Cipero Formation at about the *Globorotalia fohsi lobata*/*G. fohsi robusta* zone transition, showed the test, in dorsal view, to have as many as twelve chambers.

G. ruber has hitherto been regarded as a single species ranging from the early to Middle Miocene to Recent (Bolli 1957, p. 114). Bronnimann (in Todd *et al.* 1954) described a

new species, *G. subquadratus*, from Saipan and the Cipero Formation, Trinidad. It is not clear from this work whether or not Bronnimann considered that both *G. subquadratus* and forms later described by Bolli (1957) as *G. ruber* could be recognized in the Cipero. Bronnimann made no comparison between his species and *G. ruber* but Bolli (1957) considered *G. subquadratus* from the Cipero a junior synonym. The present paper demonstrates morphological differences between early to Middle Miocene forms (described from Trinidad as either *G. subquadratus* or *G. ruber* (Bronnimann 1954; Bolli 1957) and those from the Pliocene and younger deposits, generally referred to as *G. ruber*. Therefore it is proposed that the name *G. subquadratus* be used for the early to



TEXT-FIG. 1. Series of specimens illustrating the ontogeny of *G. ruber* and *G. subquadratus*. *a-d*, *G. ruber*; *a*, No chambers removed; *b*, Four chambers removed; *c*, Five chambers removed; *d*, Six chambers removed and showing four chambers in ventral view; late Pleistocene, Niger Delta, $\times 140$. *e-h*, *G. subquadratus*; *e*, No chambers removed; *f*, One chamber removed; *g*, Two chambers removed; *h*, Penultimate whorl, the final whorl of three chambers removed; from type locality of *G. insueta* zone, Trinidad. All $\times 60$, BMNH P46606-15.

Middle Miocene forms. This species is redefined on the basis of observations more fully discussed below. The use of the name *G. ruber* is restricted to the Pliocene to Recent forms. Where a discussion of the gross morphology of both these species is concerned (and particularly with reference to the chamber arrangement in the final whorl) the term '*G. ruber* s.l.' is used.

Banner and Blow (1960) distinguished *G. ruber ruber* and *G. ruber subquadratus*, the latter being the ancestral form. However, the writer regards these morphological differences as constituting ordinary variation. Their lectotype (of *G. ruber*) is therefore considered to apply only to the Uppermost Miocene to Recent forms. The type figures (Banner and Blow 1960, pl. 3, figs. 8*a*, *b*) clearly show the three-chambered penultimate whorl typical of many of these younger forms. The proloculus appears abnormally large (pl. 3, fig. 8*a*) and probably additional initial chambers occur, but could not be observed due to thickening of the test over the apical area.

SYSTEMATIC DESCRIPTION

Globigerinoides subquadratus Bronnimann

Plate 103, figs. 2-4

1954 *Globigerinoides subquadratus* Bronnimann in Todd *et al.*, p. 680, pl. 1, figs. 5, 8.1957 *Globigerinoides rubra* d'Orbigny; Bolli, p. 113, pl. 25, figs. 12a-13b, text-fig. 21, no. 6.

Description. Test moderately large, consisting of proloculus followed by whorl of four or possibly five chambers, a second (or penultimate) whorl of four chambers, gradually and uniformly increasing in size, and a final whorl of three chambers. Periphery varies from lobulate to quadrate in outline. Primary aperture usually large, interiomarginal, umbilical, and situated symmetrically with respect to the penultimate and antepenultimate chambers. Two dorsal supplementary apertures are present at the base of the final chamber, and one at the junction of the basal suture and the intercameral suture of the preceding whorl. Umbilicus shallow. Wall radiate calcareous, frequently thickened, with a slightly rugose surface.

Remarks. The essential difference between *G. subquadratus* and *G. ruber* is in their ontogeny. The former has a penultimate whorl of four chambers (Pl. 103, figs. 2a, 3, 4), while the latter consists of a penultimate whorl of three chambers, with the final chamber of the initial whorl to a greater or lesser extent forming part of it (cf. Pl. 103, figs. 2a, 3, 4

EXPLANATION OF PLATE 103

Fig. 1 a, b. *Globigerinoides subquadratus* s.l. a, dorsal view; b, ventral view. From type locality of *G. stainforthi* zone, Cipro Coast, Trinidad. BMNH P46593, $\times 113$.

Figs. 2 a, b-4. *Globigerinoides subquadratus* Bronnimann 1954. a, Dorsal view; b, Ventral view; Sample ER 577, *G. insueta/bisphericus* zone, type section Montpelier Formation, St. James, Jamaica; BMNH P46594, $\times 117$. 3, Dorsal view; type locality of *G. folisi robusta* zone, Cipro Coast, Trinidad; BMNH P46595, $\times 110$. 4, Dorsal view; Bodjonegoro No. 1, 1,270-m. level, *Globigerinoides ruber* zone, Java; BMNH P46596, $\times 112$.

Fig. 5 a, b. *Globigerina* sp. or ?*Globigerinoides* sp. a, Dorsal view; b, Ventral view; specimen pseudo-morphing the *subquadratus/ruber* type morphology in ventral view, supplementary aperture indistinct; Sample ER 146/37, higher part of Buff Bay Formation, Jamaica; BMNH P46597, $\times 114$.

Fig. 6 a, b. *Globigerinoides* sp. a, Dorsal view; b, Ventral view; specimen showing general similarity to the *subquadratus/ruber* type morphology; Sample ER 143/37, higher part of Buff Bay Formation, Jamaica; BMNH P46598, $\times 114$.

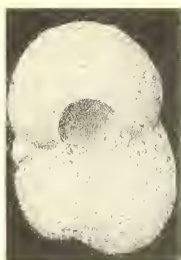
Figs. 7-10. *Globigerinoides ruber* (d'Orbigny 1839.) 7a, Ventral view; 7b, Dorsal view, specimen showing fourth chamber in the penultimate whorl; Bodjonegoro No. 1, 308-m. level, Pliocene, Java; BMNH P46599, $\times 102$. 8, Dorsal view; specimen showing fourth chamber only just entering penultimate whorl; Bodjonegoro No. 1, 308-m. level, Pliocene, Java; BMNH P46600, $\times 121$. 9a, Ventral view; 9b, Dorsal view; Pacific Core CAP 38 BP at 460-463 cm., Pliocene; BMNH P46601, $\times 110$. 10a, Dorsal view; 10b, Ventral view; showing three-chambered penultimate whorl, details of the initial whorl not seen; late Pleistocene, Niger Delta; BMNH P46602, $\times 110$.

Figs. 11-13, 15. *Globigerinoides ruber*, dissected specimens with the last three chambers (i.e. final whorl) removed. 11, 12, Showing four chambers ventrally; 13, 15, only three; Bodjonegoro No. 1, 308-m. level, Pliocene, Java. 11, BMNH P46603; 12, BMNH P46604; 13, BMNH P46605; 15, BMNH P46837. All approx. $\times 100$.

Fig. 14. Dissected specimen of *G. ruber* with three chambers removed; Pacific Core CAP 38 BP at 460-463 cm., Pliocene; BMNH P46606; $\times 80$.



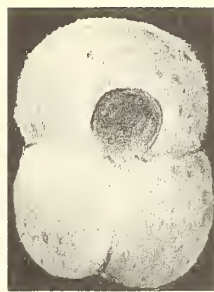
1a



1b



2a



2b



3



4



5a



5b



6a



6b



7a



7b



8



9a



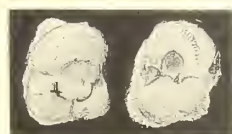
9b



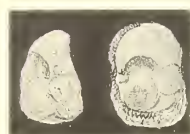
10a



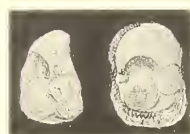
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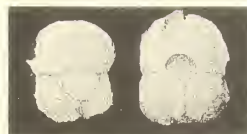
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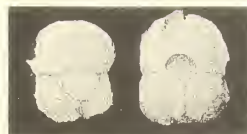
11b



12a



12b



13a



13b



14



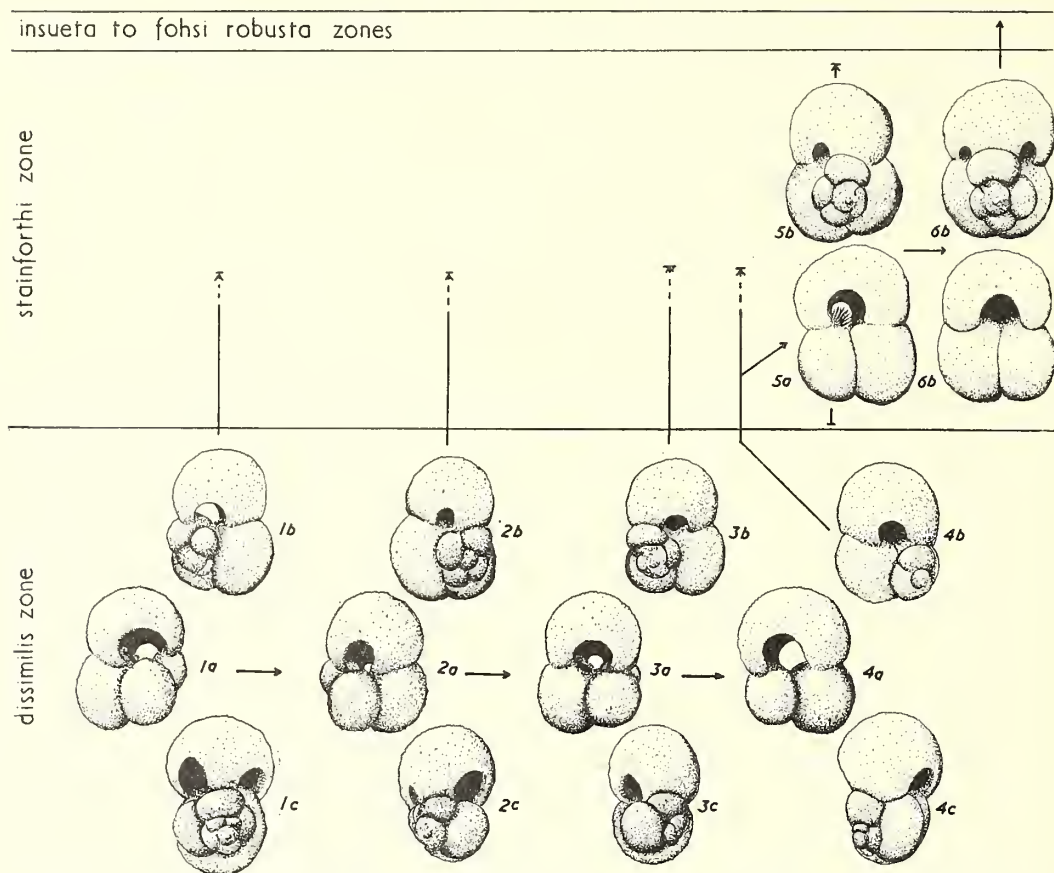
15

with Pl. 103, figs. 7a, 8, 9b); in the following discussion this is termed a whorl of $3\frac{1}{2}$ chambers. However, this fourth chamber is invariably much smaller than the remainder of the chambers in this whorl and thus differs from the relative size of each chamber in the penultimate whorl of *G. subquadratus*. This appears to be a character useful in distinguishing the two species. The other chamber arrangement in *G. ruber* is one in which there are only three chambers in the penultimate whorl (Pl. 103, fig. 10a). Therefore in *G. subquadratus* removal of three chambers invariably produces a form with four chambers present (Pl. 103, fig. 11; text-fig. 1h). However, in *G. ruber* upward of four chambers (frequently six) can be removed before four chambers are seen in ventral view (Pl. 103, fig. 14; text-fig. 1g). Many of the specimens in which there is a fourth chamber in the penultimate whorl in dorsal view, when dissected still show the three-chambered whorl (Pl. 103, fig. 15). However, exceptions occur (Pl. 103, figs. 12, 13) but this fourth chamber is only just visible (cf. Pl. 103, fig. 11 with figs. 12, 13). These latter forms are discussed further in the section on *Bodjonegoro* below.

Globigerinoides subquadratus in *Trinidad*. Bolli (1957) recorded *G. ruber* (i.e. *G. subquadratus* here defined) from the *Globigerinita dissimilis* to the *G. fohsi robusta* zones. Specimens from the type locality of the *G. dissimilis* zone show a chamber arrangement consisting of a proloculus followed by four or five chambers, and a second whorl of four chambers, all of which show a gradual and uniform increase in size as in a typical *Globigerina*. This is followed by a final whorl of three chambers, arranged in the typical tricamerate mode (Pl. 103, figs. 1a, b). The primary aperture, however, was never seen to be absolutely symmetrically placed with respect to the penultimate and antepenultimate chambers (text-fig. 2, 4a) as in a typical *G. subquadratus*. Examination of the dorsal side showed a single large supplementary aperture at the base of the final chamber, and above the third chamber of the penultimate whorl (text-fig. 2, 1-4). Approximately 70% of the forms were coiled dextrally.

There appears to be continuous variation between these specimens (i.e. *G. ruber* of Bolli 1957) and forms referable to *Globigerinoides quadrilobatus altiaperturae* (Bolli 1957), and the former are evidently extreme variants of the latter, which are far more numerous. This development is the result of the coiling becoming looser, so that the final chamber is in contact with penultimate and antepenultimate chambers as in typical *G. ruber* s.l. (text-fig. 2). A marked change in the morphology is seen in the succeeding zone of *G. stainforthi*. The extreme variants of *G. quadrilobatus altiaperturae* described from the *G. dissimilis* zone are still present, but the primary aperture is now truly symmetrically placed with respect to the penultimate and antepenultimate chambers (text-fig. 2, 5a). These forms were not observed above the *G. stainforthi* zone. There are, in addition, forms which differ from the extreme variants of *G. quadrilobatus altiaperturae* in several ways. They possess two supplementary apertures, instead of one, at the base of the final chamber (text-fig. 2, 6b). Additional supplementary apertures on earlier chambers are present, but an exact count is rendered difficult by poor preservation. These are regarded as *G. subquadratus* s.s. The proloculus is followed by whorls of five, four, and finally three chambers, i.e. as seen in the previous zone (Pl. 103, figs. 2a, b). The proportions of forms with a single supplementary aperture and those with two is about equal, with sinistrally coiled forms dominating in the former, and dextral in the latter. The same transition from *G. quadrilobatus altiaperturae* was also seen.

The succeeding zone of *Globigerinatella insueta* is characterized by a predominance of *G. subquadratus* with two supplementary apertures, while those with only one now constitute only a very small percentage (about 2%) of the fauna, and sinistrally coiled forms dominate. Occasionally the final chamber of the penultimate whorl shows a



TEXT-FIG. 2. Diagram to illustrate the variation of the *G. quadrilobatus altiapturus*–*G. subquadratus* series in the type localities of the *G. dissimilis* and *G. stainforthi* zones of Trinidad. 1a–c, 2a–c, *G. quadrilobatus altiapturus*; 3a–c, Intermediate forms; 4a–c, 5a–c, *Globigerinoides subquadratus* s.l.; 6a–c, *Globigerinoides subquadratus* s.s. All $\times 50$. BMNH P46616–21.

marked increase in size over the one before, but the majority of specimens have a penultimate whorl of four chambers gradually and uniformly increasing in size.

In the succeeding zones of *G. fohsi barisanensis*, *fohsi fohsi*, *fohsi lobata*, and *fohsi robusta*, *G. subquadratus* is in all respects identical to the *insueta* forms, the penultimate whorl consisting of four chambers. There is not such a gradual increase in chamber size as previously observed in the penultimate whorl, and the final chamber is often markedly larger than the preceding one.

The lack of specimens in the younger deposits considerably handicapped the study. However, the group reappears in the Upper Miocene Melajo Formation, but the

specimens (now regarded as *G. ruber*) are often small. They appear to be juveniles since they are exactly equivalent in size to the first and second whorls of much larger specimens. The chamber arrangement appears to be an initial whorl of five chambers followed by three.

Occasional specimens of *G. ruber* (as here defined) are seen in the Pliocene Talparo Formation. The test most probably consists of an initial whorl of five chambers, but thickening, and the lack of sufficient numbers of specimens, prevent an accurate count. This is followed by two whorls of three chambers each.

Therefore, it appears that *G. subquadratus* arises from *G. quadrilobatus altiaperturae*, the first indication occurring in the *dissimilis* zone, where it is very much an extreme variant of the latter species. *G. subquadratus* s.s. first appears in the *stainforthi* zone, being characterized by the presence of two supplementary apertures at the base of the final chamber. The precise limits of *G. quadrilobatus altiaperturae* are subjective, and it is a matter of choice whether the extreme variants of this species (text-fig. 2) are regarded as a distinct species or subspecies. The writer refers those forms with three chambers visible in ventral view, and having a single supplementary aperture, to *Globigerinoides subquadratus* s.l. (text-figs. 2, 4, 5). It is considered that the range of *G. subquadratus* s.s. in Trinidad is *G. stainforthi* zone to the *G. fohsi robusta* zone, and not *G. dissimilis* to *G. fohsi robusta* zone as given by Bolli (1957).

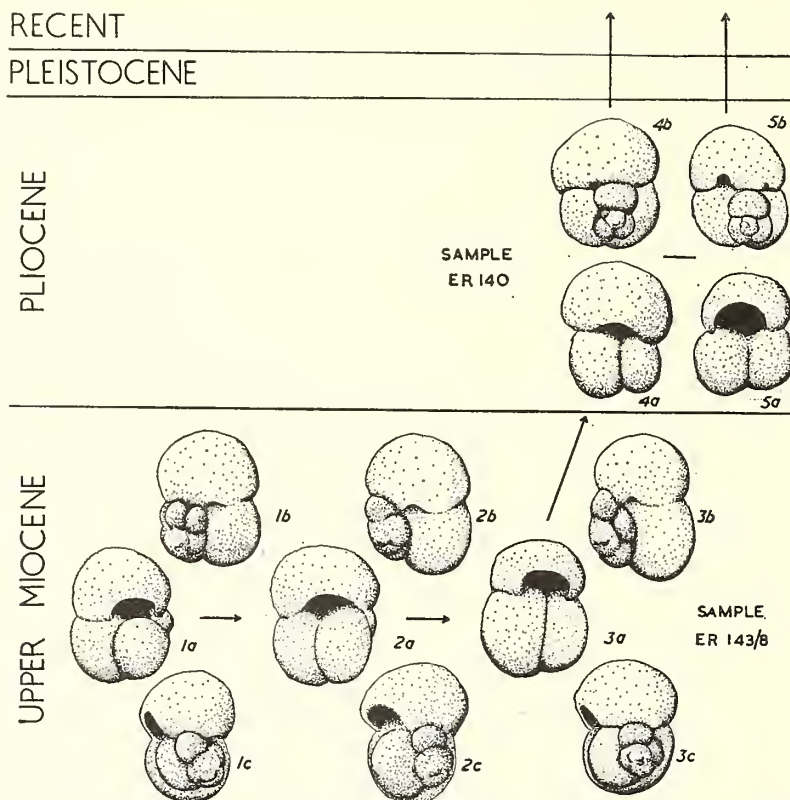
Blow and Banner (*in* Eames *et al.* 1962) suggest that *G. subquadratus* (i.e. *G. ruber*) could develop from *Globigerina woodi* Jenkins 1965. In the writer's opinion this may be correct only in that *G. woodi* could have given rise to *G. quadrilobatus altiaperturae*. In terms of morphology the latter is considered the closest ancestral form to *G. subquadratus* (see Jenkins 1965).

G. subquadratus in Jamaica. Samples were examined from several levels ranging in age from the Miocene *insueta* zone to the Pleistocene. A few specimens of *G. subquadratus* were obtained from a sample (ER 518) thought to be low in the *insueta* zone. Preservation was poor, and the initial chamber arrangement could not be determined. However, two specimens were obtained, which had only a single supplementary aperture and therefore were similar to specimens obtained from the *dissimilis* and *stainforthi* zones of Trinidad. One specimen with two supplementary apertures was found.

A sample (ER 577) from the type section of the Montpelier Formation, north of Montpelier, of *G. insueta/bispherica* zone age was examined. This showed a chamber arrangement identical with material from the *insueta* zone of Trinidad described above. The coiling was equally divided between dextral and sinistral. A sample from near the top of the Montpelier Formation, Buff Bay section, in the zone of *G. fohsi robusta*, yielded a few specimens of *G. subquadratus* which were identical with specimens described above from Trinidad.

A sample (ER 146/33A) low in the Buff Bay Formation yielded no specimens of the group. Another sample (ER 146/37) higher in this formation yielded a few specimens which had a morphology similar to the *ruber* group (Pl. 103, figs. 5, 6). These specimens are not considered to belong to *G. ruber*, but are regarded as either abnormal forms, or possibly extreme variants of some other species. Similar forms have occasionally been observed in the Lengua Formation of Trinidad. An Upper Miocene sample (ER 143/8) from the lower part of the San San Member, Bowden Formation, yielded a number of

specimens which possessed a primary aperture, varying from a symmetrical to a slightly asymmetrical position. Only one supplementary aperture was present, four chambers in the penultimate whorl, and three in the final one (details of the initial whorl could not be determined owing to thickening of the test). Furthermore, there appears to be a



TEXT-FIG. 3. Diagram to illustrate the suggested development of *G. ruber* from a form similar to *G. obliquus* Bolli 1957 (fig. 1a-c) in Jamaica. 2a-c, Intermediate form; 3a-c, *G. ruber* s.l.; 4a, b, 5a, b, *G. ruber* s.s. Note the single supplementary aperture in 3b and the two apertures in 4b, 5b. Figs. 1-3 from the lower part of the San San Clay Member, Bowden Formation, San San Bay, Jamaica; BMNH P46622-5. Figs. 4, 5 from the type locality, Bowden Mollusc Bed, Jamaica; BMNH P46626-7. All approx. $\times 50$.

gradational series varying in morphology from forms similar to *Globigerinoides obliquus* Bolli 1957 to those close to *G. ruber* (text-fig. 3, 1a-3a).

This variation is interesting as it parallels (in terms of gross morphology) the variations seen in the Middle Miocene *G. dissimilis* zone of Trinidad. Here, the ancestral form appeared to be *G. quadrilobatus altiapturus*. Both series can be distinguished in terms of detailed morphology, the *altiapturus/subquadratus* series having the high inflated final chamber, while the '*obliquus/ruber*' series is characterized by the more depressed final chamber (text-fig. 3, 1a-3a).

Another sample (ER 143/21A) from the highest exposed part of the San San Clay, considered to be approximately at the level of the Miocene-Pliocene boundary, yielded

only two specimens of *G. ruber*. One possessed a single primary aperture, the other had two such apertures. The latter appeared to have an initial whorl of five chambers followed by $3\frac{1}{2}$ and finally 3 chambers.

A Pliocene sample (ER 140) from the type locality of the Bowden Mollusc Bed yielded a number of specimens. The details of the initial chamber arrangement could not be determined owing to poor preservation. The penultimate whorl was comprised of 3 or $3\frac{1}{2}$ chambers. However, it would appear that in the case of specimens with a penultimate whorl of $3\frac{1}{2}$ chambers in dorsal view, only 3 are visible ventrally, as in a typical specimen of *ruber*. This differs from the Middle Miocene material, from both Trinidad and Jamaica, where specimens with a 4-chambered penultimate whorl, when dissected and examined ventrally, clearly showed 4 chambers (text-fig. 1*h*) and not 3 with a fourth just visible as in the case of the younger material (cf. Pl. 103, figs. 11, 12). All specimens possessed two supplementary apertures in the final chamber.

This same morphology was seen in a younger sample (ER 536) from the Bowden Formation, Folly Point section. The number of specimens with 3 or $3\frac{1}{2}$ chambers in the penultimate whorl was about equal, and the proportion of dextrally and sinistrally coiled specimens was also equal.

Finally a series of specimens were examined in a Pleistocene sample (ER 150) from the Navy Island Member of the Manchioneal Formation, exposed in San San Bay. All specimens possessed 2 supplementary apertures in the final chambers, and 27 out of 30 specimens had a penultimate whorl of 3 chambers only, followed by a final whorl of 3.

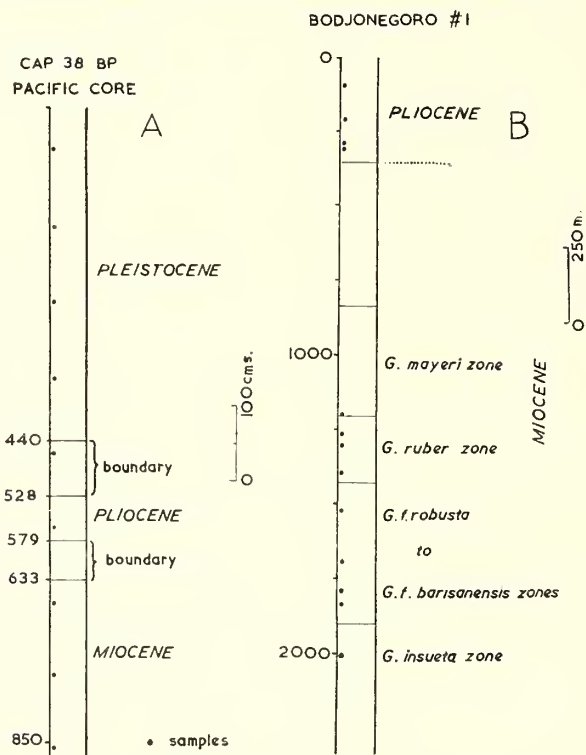
Java, Bodjonegoro No. 1. The benthonic foraminifera have been described by Boomgaard (1949), and the planktonics by Bolli (1966). Material was examined from thirteen levels, a total of about eighty specimens in varying states of preservation. The stratigraphic details are given in text-fig. 4*B*.

The range of *G. subquadratus* in Java is thus slightly greater than in Trinidad, since according to Bolli (1966) the *G. ruber* zone lies above the *G. fohsi robusta* zone, the former zone being absent in Trinidad.

The Middle Miocene specimens (i.e. *Globigerinatella insueta* to *Globigerinoides ruber* zone) all possessed five chambers in the initial whorl, followed by four chambers in the penultimate whorl. All specimens possessed two supplementary apertures in the final chamber.

The species, as in Trinidad, and apparently the Caribbean area generally, is absent in the remainder of the Miocene, reappearing in the Pliocene. These Pliocene forms all show either $3\frac{1}{2}$ and less frequently 3 chambers in the penultimate whorl, and 2 supplementary apertures. Specimens from the 308-m. level were dissected, and removal of the final whorl showed the typical *G. ruber* s.l. type of chamber arrangement. However, the removal of the final whorl of some specimens showed a four-chamber arrangement (Pl. 103, figs. 12, 13, 15). These forms, therefore, have an ontogeny similar to that described for *G. subquadratus*. However, it is suggested that *G. ruber* arose from an ancestral form similar in gross morphology to *G. obliquus* Bolli 1957 and it is reasonable to expect that such forms would persist for a time. With these forms were specimens in which up to 6 chambers were removed before a 4-chambered whorl was observed (Pl. 103, fig. 14). These were never observed in the Middle Miocene *G. subquadratus* Bronnimann 1954 described above.

Pacific Core, CAP 38 BP. 14° 16' S., 119° 11' W. (water depth 3,400 m.). Samples from this core, representing sediments of Upper Miocene to Pleistocene age, were examined at eight levels (text-fig. 4). The greatest numbers of specimens were obtained in samples from the 460- and 360-cm. levels. All specimens of *ruber* had two supplementary apertures on the final chamber, and no ancestral forms were observed.



TEXT-FIG. 4. A, Stratigraphic details of Pacific Core CAP 38 BP (after F. L. Parker). B, Stratigraphic details of Bodjonegoro No. 1 (after H. M. Bolli).

Although fewer specimens were obtained from samples below the 460-cm. level, there is a fairly even distribution of forms with $3\frac{1}{2}$ and 3 chambers in the penultimate whorl. However, in samples at 460 cm. and 360 cm. there is an appreciable change in the proportions, the three-chambered forms being dominant. Whether or not this trend becomes firmly established could not be definitely determined, owing to lack of specimens at the highest levels. Two samples supplied by Dr. W. H. Blow from the Niger Delta, and considered by him to be late Pleistocene, showed that three-chambered forms were dominant (text-fig. 1 a-d). A few Recent samples were examined, and these also indicated the dominance of three-chambered forms. The coiling ratios in the Pacific Core material were equally divided between dextrally and sinistrally coiled forms, with the exception of the 261-cm. level, where dextrally coiled specimens dominated. However, only thirteen specimens were obtained and this is a possible explanation for the change.

The evidence from the Upper Miocene to Recent material examined suggests the following conclusions. Initially, forms with 3 and $3\frac{1}{2}$ chambers in the penultimate whorl occur. Certain of the latter on removal of the final whorl show four chambers present in ventral view (Pl. 103, figs. 12, 13, 15). At successively higher levels, the three-chambered forms become more dominant, with the accompanying change in the ontogeny described above. This appears to take place in the late Pliocene or early Pleistocene. Therefore, the separation of the species *G. ruber* from *G. subquadratus* (as here defined) is not based on the morphology of any single specimen of the former, but rather on the morphological development of an assemblage of specimens.

The writer considers that the forms here referred to as *G. subquadratus* and *G. ruber* constitute two separate and unrelated lineages, since:

- (a) There is a break in the range of the *subquadratus/ruber* group in widely separated parts of the world. This is more suitably explained by regarding the forms as constituting two lineages, rather than postulating unfavourable environment as an explanation for the break (cf. Bolli 1957).
- (b) *G. subquadratus* in the *G. fohsi robusta* zone in Trinidad and Jamaica, and in the *G. ruber* zone in Java, possesses two supplementary apertures at the base of the final chamber. When forms with a similar morphology reappear in late Miocene times, they at first possess a single supplementary aperture (text-fig. 3, 1a-3a). This parallels a similar development in the ancestral form of *G. subquadratus*, here considered to be *G. quadrilobatus altiaperturae*.
- (c) There is evidence to suggest that *G. ruber* in the Uppermost Miocene of Jamaica was derived from a form similar to *G. obliquus* in gross morphology. *G. subquadratus* is thought to have developed from *G. quadrilobatus altiaperturae* (Bolli 1957).
- (d) Details of ontogeny are, with few exceptions, quite different in the two lineages.

CONCLUSIONS

An examination of forms previously regarded as belonging to the single species *Globigerinoides ruber* d'Orbigny from widely separated localities, representing its entire stratigraphic range, indicates the following:

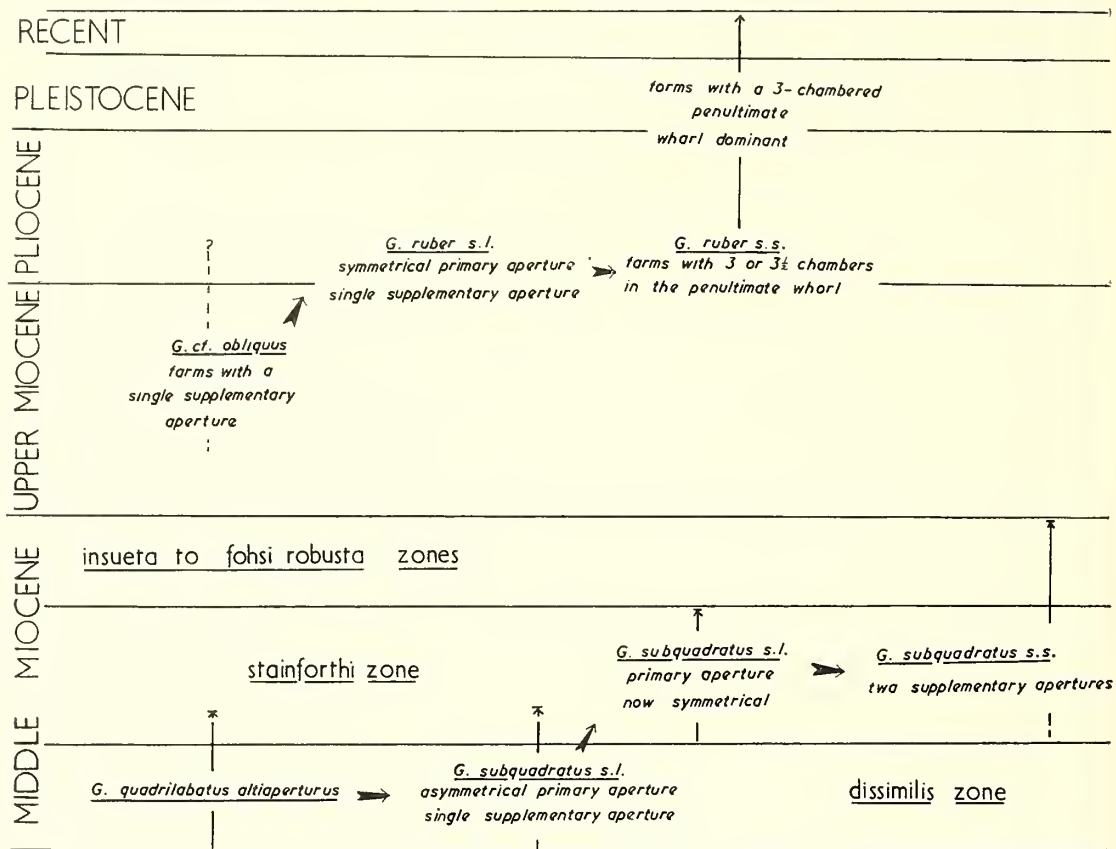
1. The existence of two unrelated lineages, one in the early to Middle Miocene, the other in the Uppermost Miocene (or basal Pliocene) to Recent.

2. Evidence from the *G. dissimilis* zone in Trinidad suggests that the ancestor of the early to Middle Miocene forms is *Globigerinoides quadrilobatus altiaperturae*, *G. subquadratus* s.s. occurring first in the succeeding zone of *G. stainforthi*. Specimens from the Uppermost Miocene San San Member, Bowden Formation, Jamaica, suggest that the younger lineage could have arisen from an ancestor similar in gross morphology to *Globigerinoides obliquus*. This is therefore an example of heterochronous homeomorphy.

3. It is proposed that the species name *Globigerinoides subquadratus* Bronnimann 1954 be used for the early to Middle Miocene forms and *Globigerinoides ruber* (d'Orbigny 1839) for the Uppermost Miocene (or Pliocene) to Recent forms.

4. An examination of the wall reveals a variation in structure, but this was not considered to be of stratigraphic importance, and there appears to be no significant difference in this respect between the two lineages.

5. Insufficient numbers of specimens at many levels prevent any definite statement as to the value of coiling ratios in the group as a whole. In specimens from the Cipero



TEXT-FIG. 5. Suggested phylogeny of *G. subquadratus* and *G. ruber*.

Formation the ratio of dextral to sinistral is not constant, whereas in the Pliocene-Pleistocene material from Jamaica and the Pacific Core CAP BP 38, the ratios were generally equally divided between the two directions of coiling.

6. *G. subquadratus* s.s. is considered to have its first occurrence in the *stainforthi* zone (cf. Bolli 1957), the *subquadratus*-like variants are included in *G. subquadratus* s.l., and these forms do not range above the *insueta* zone in Trinidad.

7. The forms described above have previously been regarded as a single long-ranging species, but it is suggested that this morphological group can be subdivided, and certain developmental trends have been noted. An alternative explanation to Bolli's (1957,

1966) view that these forms represent a single species (*G. ruber*) which is absent in the Middle–Upper Miocene owing primarily to environmental factors, is also put forward.

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THE SEQUENCE AND DISTRIBUTION OF LUDLOVIAN, LOWER DEVONIAN, AND COUVINIAN CORAL FAUNAS IN THE UNION OF SOVIET SOCIALIST REPUBLICS

by D. HILL

ABSTRACT. The records of coral faunas in the U.S.S.R. are summarized and some suggested synonyms mentioned. The distribution of the faunas is discussed and characteristic faunal elements for the different horizons are given. In particular, first and last occurrences of genera are noted as these may be of stratigraphical value.

THIS review has been facilitated by several recent Russian reviews (Dubatolov 1964, Spasskiy 1964, Kal'o 1965, Nikiforova and Obut 1965, and Ivanovskiy 1965*b*), but is based in the main on the very numerous papers descriptive of the Ludlovian, Lower Devonian, and Couvinian corals of the U.S.S.R.

Russian coral taxonomy has a somewhat different tradition from that of Europe and America, but I have attempted some reconciliation by suggesting changes in published taxonomy. Russian evaluation of the genera of tabulate corals seems to me to be superior to that of western usage and I have in general adopted it herein. I apologize to my Russian colleagues for any misrepresentations of their views; any such are due to my poor knowledge of Russian. I thank them for their generosity in supplying reprints.

LUDLOVIAN, SKALIAN, and TIVERIAN

Ludlovian, when not qualified, is taken in this review to mean the time of development of the faunas in the post-Wenlockian strata of England deposited before the Ludlow Bone Bed. In Horny's view (1962) this corresponds approximately with the Kopanina Beds of Czechoslovakia. Skalian implies the time of development of the faunas of the Skala beds of Podolia which may or may not be equivalent in age to the Ludlow Bone Bed and perhaps to part of the Downtonian, and may correspond approximately with the Pridoli Beds of Czechoslovakia containing graptolite zones *P. ultimus* to *M. angustidens*. Tiverian implies the time of development of the faunas of the Borszczow and Czortkow beds of Podolia, and by indirect correlation is regarded as approximately equivalent to the Lochkovian of Czechoslovakia. The Lochkovian faunas, by the graptolite correlations of Jaeger (1962, 1965) and the range of *Hysterolites hystericus* (Schlothheim) as established by Solle (1963), are taken to be time equivalents of the Gedinnian and much of the Siegenian of Belgium and Germany. For discussions on the equivalence of the base of the Lochkovian to the base of the Gedinnian see also Alberti (1962, 1963), Boucot (1960), Boucot and Pankiowskyj (1962), Hollard (1963, 1965), and Walliser (1962, 1964). The Pragian of Czechoslovakia is considered roughly equivalent to the remaining Upper Siegenian plus Lower Emsian time as is the Zlichovian of Czechoslovakia to Upper Emsian time. Couvinian and Eifelian stages are regarded as

approximately equivalent, though it is recognized that the Lower Couvinian (Co₁ of Belgium) may have begun slightly earlier than the Lauch Beds of the Eifel. It would appear from the table given by Erben (1962) that the zone of uncertainty may have narrowed to Co_{1a}; Erben suggests that Co_{1a} may be broadly equivalent to the Heisdorf Beds and a part of the underlying Wetteldorf Beds of the Prum Syncline; the Heisdorf Beds he considers topmost Emsian.

It is believed that justification for these working correlations exists as a result of the Prague (Svoboda, Horny, and Chlupac 1960) and Bonn (Erben 1962) symposia on the boundary between the Silurian and Devonian systems and the colloquium on the Lower Devonian and its limits held in Rennes in 1964 ('Colloque', 1965), and of the subsequent literature, including Hollard (1965).

In the U.S.S.R. the common usage of Lower Ludlovian corresponds reasonably with 'Ludlovian' as defined above, but possibly includes Skalian in some sequences; while the Russian 'Upper Ludlovian' has recently (Nikiforova and Obut 1965) been correlated with the Tiverian of Podolia. In some places it may also include the Skalian.

Podolia

Here the Rugosa of the Malinovetski Formation appear to be Ludlovian as Boucot and Pankiwskyj (1962a) suggested, rather than Wenlockian as previously accepted (Rózkowska 1946). They include *Weissermelia lindstromi* (Smith and Tremberth) which is illustrated elsewhere at present only from the Hemse group of Gotland and the Ludlovian of Tuva (Soshkina, Dobrolyubova, and Kabakovich 1962), but is reported by Bulvanker (1952) also from the Skala of Podolia. The rest of the Rugosa illustrated by Bulvanker (1952) and by Ivanovskiy (1965a) are consistent with a Ludlovian age and the fauna bears a general resemblance to that of the *M. leintwardinensis* zone of England. It consists of *Phaulactis*, *Pilophyllum*, *Rhabdocyclus minimus* (Bulvanker), solitary *Tryplasma*, *Aphyllum* (phaceloid *Tryplasma*?), *Cystiphyllum* including '*Microplasma*', *Holmophyllum*, and *Rhizophyllum*. Boucot and Pankiwskyj (1962b) listed *Favosites*, *Alveolites*, *Coenites*, *Thecia*, *Heliolites*, *Halysites*, *Aulopora*, and *Syringopora*. *Halysites* is not listed by them from younger formations in Podolia. According to Sokolov (1962d) and Sokolov and Tesakov (1963, p. 124) in the upper Malinovetski horizon there is a distinctive new genus of alveolitoid corals without pores, very common in the Kopanina beds of Czechoslovakia and in the 'Lower Ludlow' of Central Asia; they also state that the upper beds of the Malinovetski horizon and the Skalian horizon have predominant *Favosites* with rare *Squameofavosites*, *Subalveolites*, *Taxopora*, and the last Halysitidae, with *Syringopora* and small thamnoporids. Earlier descriptions are in Venyukov (1899) and Semiradski (1906).

The Skalian Rugosa (Bulvanker 1952, Ivanovskiy 1965a) are *Dokophyllum*, *Spongophylloides*, *?Acanthophyllum nikiforovae* (Bulv.), solitary *Tryplasma* (as *Pholidophyllum* and *Stortophyllum*), fasciculate *Tryplasma* (as *Aphyllum*), three species referred by Bulvanker to *Holmophyllum* but which do not appear to me to be congeneric with *H. holmi*, the type species. Bulvanker recorded *Phaulactis cyathophylloides* Ryder and *Weissermelia lindstromi* (Smith and Tremberth) but did not figure them. *A? nikiforovae* would seem to indicate that Devonian solitary ptenophyllids developed from the Silurian *Spongophylloides*, for this species seems related to the species group *S. perfectus* (Wedekind). This rugosan fauna is certainly still closely related to that of the Ludlovian.

Rózkowska (1946) described some of the Rugosa of the Tajna beds of Mazurowka which according to Boucot and Pankivskyj (1962) include both Skala and Borszczów horizons. Her list is *Spongophylloides grayi* (E. & H.), *S. perfectus* (Wdkd.), *Tryplasma loveni* (E. & H.), *Cystiphyllum* (as *Microplasma*), and *Rhizophyllum gotlandicum* (Roemer). Bulvanker (1952) figured *Phaulactis* from the Borszczów horizons.

Skala Tabulata are considered by Klaaman (1965, p. 38) to indicate that the Skala is of the same age as the Estonian 'Lower' Ludlow (Kaarma to Ohesaare stages). He does not list the Skala fauna, but states that in the overlying Borszczów only *Pachyfavosites kozłowski* Sokolov (1955, pl. 4) occurs in abundance and that in Gotland the Burgsvik, Hamra, and Sundre horizons at the top of the Gotlandian form a zone of *Pachyfavosites*. He thus deduces that the Tiverian (Borszczów and Czortków horizons of Podolia) is equivalent to the Burgsvik, Hamra, and Sundre. Supporting evidence is necessary before his correlations can be regarded as established. According to Sokolov and Tesakov (1963, p. 124) the Skalian and upper Malinovetski horizons have *Favosites* predominant, with rare *Squameofavosites* and *Subalveolites*. Dubatolov (1963, p. 139) says that *Multisolenia* makes a late appearance in the Skalian of Podolia with *Squameofavosites* but he does not figure it.

The Skalian coral faunas are too little known at present for precise definitions. Present records suggest that *Squameofavosites* and *Thamnopora* entered therein (or in the Lower Ludlow? Upper Malinovetski horizon). Whether the Skalian is Gedinnian or pre-Gedinnian is still for discussion.

We lack definitive studies of the Tiverian (Borszczów and Czortków) corals of the type area in Podolia. The *Phaulactis* figured from the Borszczów by Bulvanker (1952) seems correctly referred to that Silurian genus. Sokolov and Tesakov (1963, p. 128) remark that in Podolia the first representatives of *Pachyfavosites* are characteristic for the Tiverian with extremely rare *Pleurodictyum* and a new genus of alveolitoid corals without pores (Sokolov 1962d).

Sokolov (1965, in the unpublished Bull. Ludlow Research Group, No. 12, p. 16) records a report by Obut of the discovery of a great number of *Monograptus uniformis* Přibyl in the upper part of the lower half of the Borszczów horizon, giving direct comparison with the lower Lochkovian of Czechoslovakia.

According to Tarlo (1964) the fishes of the Czortków beds are Lower Gedinnian. If this is so, probably the entire Tiverian of the type area is equivalent to only the early part of the Lochkovian. The 'Upper Ludlovian' or 'Tiverian' of the rest of the U.S.S.R. must be separately evaluated for each region for correlation with the Lochkovian and the Western European stages Gedinnian and Siegenian.

Estonia

To the north-west of the Russian platform, in Estonia, the Kaarma, Paadla, Kaugatoma, and Ohesaare horizons forming the zone of *Favosites similis* Sokolov and *F. kogulaensis* Sok. are taken by Klaaman (1965) to correlate with the Lower Ludlovian of England, and with the Klinteberg, Hemse, and Eke groups of Gotland. The characteristic complex of Tabulata in Estonia is *Favosites forbesi* E. & H., *F. effusus* Klaam., *F. pseudoforbesi* Sok., *Thecia swinderniana* (Goldf.), *Laceripora cribrosa* Eichw., *Parastriatopora commutabilis* Klaam., and *Syringopora schmidt*, but *Palaeofavosites*, *Multisolenia*, *Coenites*, and *Romingerella* also occur. Klaaman considers this fauna

to be still represented in the Skala of Podolia, but does not list the species of the latter. The Estonian tabulatan fauna has been described by Sokolov (1952a, 1955) and Klaaman (1962a, b). Halysitidae are not known in the Ludlovian of Estonia.

Unfortunately the Rugosa have not been re-studied. The illustrations of Dybowski (1873) may be doubtfully interpreted as of *Entelophyllum*, *Phaulactis*, *Micula* or *Entelophyllum* cf. *prosperum* Barrande, *Stauria*, *Strombodes*, *Tryplasma*, and *Cystiphyllum*. Ivanovskiy (1965b) listed also *Pilophyllum*, *Acervularia*, *Weissermelia*, *Kodonophyllum*, and *Holmophyllum*, but these have not been figured. No younger corals are known in Estonia.

Novaya Zemlya, Vaygach Island, and Pay Khoy

In this miogeosynclinal milieu (Cherkesov in Nikiforova and Obut 1965), the Lower Ludlovian of Novaya Zemlya contains *Favosites* and *Heliolites* and that of Pay Khoy has graptolites. That of Vaygach Island has *Spongophylloides perfectus* Wdkd. and *Pholidophyllum vermiculare* Wdkd. (Strel'nikov 1965a, b). The overlying Grebeni and Vaygach horizons are together correlated with the Tiverian but Chekhovich (1965) suggests that the Grebeni horizon, widespread also in the Subpolar and Polar Urals, correlates with the Burgsvik-Hamra-Sundre succession of Gotland, and that only the Vaygach horizon of the Sub-polar Urals would correlate with the Tiverian. The Grebeni horizon of Novaya Zemlya contains *Parastriatopora* and *Favosites*, while on Vaygach it contains *Microplasma*, *Favosites*, *Squameofavosites*, and *Syringopora*. The overlying Vaygach horizon on Vaygach contains *Favosites*. The corals of this region have been described by Lindström (1882), Tchernyshev and Yakovlev (1898), Cherkesov (1932), and Chernyshev (1937a, 1938a, b).

Urals

Chernova Uplift. In the Chernova structure that reaches the coast at Sin-kin Nos (Barskaya 1965) the late Silurian to Tiverian has four coral faunal complexes; the earliest of these is characterized by *Parastriatopora* and the second and third by *Thecia* and *Laceripora*, though *Thecostegites* enters in the third, in what may be its earliest appearance anywhere. The fourth has *Squameofavosites*, *Favosites*, *Riphaeolites*, *Thecostegites*, and *Syringopora*. The fourth complex may be Lochkovian; perhaps the third is Skalian; the others seem equivalent to the Ludlovian of Estonia. Strel'nikov (1964) described *Stereoxylodes argutus* from the 'Upper Ludlovian'.

Polar and Sub-polar Urals. In the Sub-polar Urals that lie subparallel to and a little west of the Polar Urals, Chekhovich (1965) recognized (in the Rivers B. Sunya and Kzhim) a zone of *Laceripora cribrosa* and *Parastriatopora arctica* (with *Favosites* and *Coenites*) as approximately equivalent to the early Ludlovian Kaarma and Paadla beds of Estonia. From this zone in the Durnayus suite Strel'nikov (1965b) reported that the Rugosa are dominated by *Spongophylloides*, *Zelophyllum*, *Pholidophyllum* (= solitary *Tryplasma*), *Stortophyllum*, and *Holmophyllum*; very rare are *Micula* and *Tenuiphyllum*; some *Tabularia* and *Dentilasma* continue from the Wenlockian and *Stereoxylodes* occurs. Illustrations are not yet available.

Above this, in the lower part of the Into-Parm suite is a zone of *Favosites pseudo-forbesi ohesaarensis* and *Howellella pseudogibbosa*, which Chekhovich (1965) equated with the Grebeni horizon of Vaygach Island. *Favosites*, *Parastriatopora*, *Striatopora*?,

Table I. Main stratigraphic or biostratigraphic units mentioned in the text.

Country or Region	Suggested approximately equivalent to:-				
	Ludlovian	? Ludlow Bone Bed	Gedinnian, L & M. Siegenian	U. Siegenian and Emsian	Couvinian
Czechoslovakia	Kopanina	Pridoli	Lochkovian	Pragian & Zlichovian	Eifelian
Podolia	Malinovetski	Skala	1 Borszczow) 2 Czortkow) = Tiverian		
Estonia	1 Kaarma 2 Paadla 3 Kaugatoma 4 Ohesaare				
Novaya Zemlya	"Lower Ludlovian" Grebeni		Vaygach	Morzhov Inlet	Eifelian
Chernova Uplift	Faun. Comp. 1 & 2	F. c. 3	F. c. 4		
Polar and Sub-polar Urals	1 Durnayus 2 L. Into-Parm		U. Into-Parm		Western Slopes 1 Takatin 2 Vanyushkin 3 Vyazov 4 Calceola 5 Biya Eastern Slopes 1 "Eifelian" 2 Beds with <u>Conchidicella bashkirica</u>
Urals	see Nikiforova & Obut (1965) "Lower Ludlovian"		"Upper Ludlovian"	see Spasskiy (1959)	
Taimyr	"Lower Ludlovian"		"Upper Ludlovian"	Lower Devonian	Eifelian
Armenia					Eifelian
Tien-Shan	Dal'yan = Mustavass and Karasuy		1 Isfarin 2 Kunzhak	Akkul Dzhidalin Manak and "Coblentian"	Katran and Eifelian
Kazakhstan	Akkan f. c.		1 Aynasuy f. c. 2 Burnak f. c. "Upper Ludlovian"	Bogimbay f. c. 1 "Gedinnian" 2 "Coblentian"	Eifelian
Altai-Sayan	Potapov = Chagyr	Sukhaya	"Upper Ludlovian" Tom-chumysh = Tomskozavod = Lochtev	1 Krekov 2 Malobachat "Lower Devonian"	1 Salairkin 2 Shandin 3 Mamontov Losishin, Tashtyp, Kryukov, Sokolin, Rakitin, & Ust'-Kamen
Amur Geosyncline				1 Bolshenever 2 Imachin Il'dikan and Blagodot	
Verkhoyan - Chukotsk Geos.			Nelyudum	"Lower Devonian"	Eifelian

Numerical sequence gives ascending stratigraphic position in the stage. F. c. = faunal complex.

and *Syringopora* occur in the lower part of the zone which he correlated with the Ohesaare and Kaugatoma beds of the Estonian Ludlovian. In the upper part of the zone the above four genera are joined by the first *Squameofavosites* and *Thecostegites*; possibly this upper part may correlate with the Skalian of Podolia. The rugosan *Scyphophyllum* Strel'nikov (1964) occurs in this zone.

In the upper part of the Into-Parm suite of the Sub-polar and Polar Urals which Chekhovich (1965) correlated with the Vaygach horizon of Vaygach, and with the Tiverian of Podolia, Tabulata are rare but a zone of *Favosites socialis uralicus* and *Hebertella hebe* is recognized; Strel'nikov (1965b) reported the occurrence herein of *Orthopaterophyllum* (= *Palaeocyathus* Foerste from the highest Silurian of Yass, N.S.W.), a disphyllid (?) '*Diplophyllum*', *Spongophylloides*, and the spinose *Thecaspinellum* (a cystiphyllid with scaly? epitheca and very simple tabulae), *Pholidophyllum*, *Stortophyllum*, *Cystiphyllum* (including *Microplasna*), *Diplochone*, and *Hedstroimophyllum*. Chekhovich (1965, Table) listed *Monograptus formosus* from beds on the R. Limba considered equivalent to the base of the upper Into-Parm suite.

Northern, Central, and Southern Urals. Sytova (1952) described *Kyphophyllum elkinense* and *Entelophyllum uralicum* from the top of the Wenlockian or base of the Ludlovian of the eastern slopes of the Northern Urals. Soshkina (1937) described fasciculate *Tryplasma* and cerioid ?*Tryplasma* (as *Zelophyllum*) from 'Lower Ludlovian' strata of the miogeosynclinal zones of the western slopes; and from the eastern slopes *Entelophyllum* (as *Tenuiphyllum flexuosum* Soshk. and *Xylodes uralicus* Soshk.), solitary *Kodonophyllum*, *Stortophyllum*, fasciculate *Tryplasma* (as *Zelophyllum*), and *Rhizophyllum*. This list may well indicate a Ludlovian age. From the 'Middle Ludlow' of the western slopes cerioid '*Acervularia*' [? = *Zelolasma*], '*Pseudomphyma elongata* Wedekind', solitary *Tryplasma*, and *Stortophyllum* were described from scattered outcrops; the age is doubtful; it may be Devonian. '*Acervularia luxurians* var. *breviseptata* Weiss.' of Soshkina (1937, pl. 17) seems almost identical with *Zelolasma gemmiforme* (Etheridge) from the late Emsian or early Couvinian of eastern Australia. See Pedder (1964) for figures. From the 'Upper Ludlow' (Tiverian?) of the western slopes, possibly a new genus of solitary ptenophyllids was figured as *Omphyma*; and from the eastern slopes *Neomphyma originata* Soshkina and '*Neocystiphyllum*' [? = *Acanthophyllum*] *keyserlingi* (Dybowski). Nikolaeva (1949) described *Thecaspinellum* from the upper Silurian (Ludlovian *sensu lato*) of the Urals (R. Taltiya). I have found no recent discussion of the stratigraphy of these coralline beds, but I have deleted from Soshkina's lists those species whose holotypes were stated by Spasskiy (1960a) to be from D₂1 Eifelian and not from the Silurian, and other species listed as occurring only with these holotypes.

Taimyr

In the 'Lower Ludlow' of central Taimyr, *Favosites* and *Syringopora* occur (Zhi-zhina in Nikiforova and Obut 1965) and *Squameofavosites* was described by Barskaya (1962) from undifferentiated Ludlovian. Sokolov (1962d) reported that the 'Upper Ludlow' (Tiverian) of the Urals and adjoining islands of the Arctic and the Pechora Basin is characterized by very numerous *Squameofavosites*, *Pachyfavosites*, *Favosites* (peculiar small forms of the type of *F. socialis*), and *Syringopora*; and the first *Tetraporinus* appears.

Central Asia

Tien Shan. In this geosynclinal region in the Soviet Republics of south-east Uzbek, Tadzhik (including Pamir and Darwas), and Kirghiz, Ludlovian and Tiverian coral faunas occur in the Turkestan, Zeravshan, Gissar, Alai, Fergana, and Kirghiz ranges (Nikiforova and Obut 1965; Rukhin 1937, 1938a; Orlov 1930; Obut 1939; Chekhovich 1955a, b, c; 1956, 1961, 1964; Chekhovich *et al.* 1960; Dubatolov and Chekhovich 1964; Leleshus 1964a, 1965).

The Dal'yan horizon and the Mustavass (Yassu-Atbashin belt), Karasuy (Aksan Belt) suites correlated with it are considered Ludlovian, having *Conchidium knightii* and *Favosites*, *Squameofavosites tchernychevi* Chekhovich, *Daljanolites* Leleshus, *Heliolites*, *Helioplasmolites* Chekhovich (1955c, 1956), *Propora*, *Halysites*, and *Syringopora*. This is possibly the earliest occurrence of *Squameofavosites*. *Daljanolites* is of creeping habit, with cylindrical branches having corallites with walls thickened so that no tabulae are observed.

The Isfarin horizon with *Pholidophyllum* limestones is considered Lower Tiverian. The only rugosan I have found described is *Chavsakia* Labrusevich (1959), a large solitary cystiphylloid with scaly epitheca and coarse dissepiments and tabulae, recalling *Thecaspinellum* from the upper part of the Into-Parm suite of the Polar and Sub-polar Urals; but Sokolov (*in* Nikiforova and Obut 1965) determined *Columnaria*, *Thecaspinellum*, *Cystiphyllum*, and *Holmophyllum*. These occur with *Favosites*, *Squameofavosites*, *Pachyfavosites*, *Cladopora*, *Heliolites*, *Propora*, *Syringopora*, and *Thecostegites*. In the Dzhangdzhei Belt *Helioplasmolites* is recorded from the Isfarin horizon.

The Kunzhak horizon has *Favosites*, *Squameofavosites*, *Pachyfavosites*, and *Alveolites* and is regarded as Upper Tiverian (Dubatolov and Chekhovich 1964). In the Kunzhak beds in the Zeravshan Range occur *Monograptus hercynicus* and *M. angustidens* and in the Turkestan Range *M. ex gr. hercynicus* (*fide* Dubatolov and Chekhovich 1964, p. 8). Nikiforova and Obut (1965, p. 489) refer to a recent find of *Monograptus hercynicus* with *Paramovakia geinitziana* Bouček and *P. obuti* Bouček in the western parts of the southern Tien Shan beds, and note that this gives correlation with the Upper Lochkovian of Bohemia (i.e. probably Lower and Middle Siegenian). Pavlova (1962, 1965) has described *Fasciphyllum kokshalicum* herefrom; it has two regular series of large subglobose dissepiments in its very slender corallites. Its walls are much thinner than those of *F. conglomeratum* Schluter.

From the Chinese Tien Shan Regnéll (1941, 1961) has described a fauna that could well be Tiverian from the Arpishmebulaq series of Chol-tagh: *Cystiphyllum*, *Teratophyllum*, *Favosites*, *Angopora*, *Thamnopora*, *Striatopora*, *Alveolites*, *Heliolites*, *Plasmapora*, and *Aulopora*.

Kazakhstan

In the geosynclinal regions of Central and South-east Kazakhstan in the Karaganda basin, the Dzhungarian Alatau and the L. Balkash region, the Akkan faunal complex is considered Ludlovian; Nikolaeva (*in* Bulvanker *et al.*, 1960) has described *Ketophyllum* (very like forms from the Eke marls of Gotland considered to be *Pilophyllum* sp.) solitary *Tryplasma* and *Holmophyllum*; Nikiforova and Obut (1965) list also *Calostylis*. The Tabulata are listed by Keller (1962) and Bondarenko (1962) as *Favosites*,

Mesofavosites, *Heliolites*, and *Propora*. Kovalevskiy *et al.* (1960) and Kovalevskiy (1965) described species of *Favosites*, *Multisolenia*, *Parastriatopora*, and *Halysites*.

From the probably Tiverian Aynasuy faunal complex, Nikolaeva (*in* Bulvanker *et al.* 1960) has described the new genera *Neobrachyelasma* and *Orthopaterophyllum* (to which she refers *Streptelasma australe* (Foerste) from the Ludlovian of the Yass District, N.S.W.), and colonial *Tryplasma* (as *Zelophyllum*). Nikiforova and Obut (1965) list also *Alleyinia*, *Petraia*, *Chonophyllum*, *Oligophyllum*, *Kyphophyllum*, *Kodonophyllum*, *Neocystiphyllum*, and *Rhabdophyllum*, but of these I have found no descriptions. Keller (1962) listed *Favosites* and *Squameofavosites* herefrom and Bondarenko (1962) *Pseudoplasmapora* and *Heliolites*.

From the Burnak faunal complex above the Aynasuy complex, Keller (1962) listed *Plicatomurus* Chan (like *Pachyfavosites* but lacking fibrolamellar wall-structure); Bondarenko (1962) listed *Heliolites*, *Squameolites*, *Pseudoplasmapora*, and *Propora*. These two authors referred this complex to the middle and upper parts of the 'Upper Ludlow' (i.e. Tiverian). Descriptions of *Pseudoplasmapora* and *Squameolites* are given by Bondarenko (1963). *Pseudoplasmapora* differs from *Plasmapora* in having tubular, not dissepimental, coenenchyme. *Squameolites* has mixed tubular-dissepimental coenenchyme, and squamulae rather than septal spines. Bondarenko noted that *Plasmapora gippslandica* Chapman from the Lower Devonian of Victoria differed from the type species of *Pseudoplasmapora* only in having thickened walls to the coenenchymal tubules, this being regarded as a Devonian character.

From the Bogimbay complex, regarded as either uppermost Tiverian or basal Devonian, Keller listed *Favosites*, *Pachyfavosites*, *Squameofavosites*, *Axulites* (Sharkova 1963a, a coenitid? genus), and *Caliapora*. Barskaya and Sharkova (1963) have discussed the Tabulata of the Ludlovian of the Tarbagatay Range, and Smelovskaya (1963) the Rugosa but I have not seen their works. Also Rukhin (1939) described Upper Silurian Tabulata from near Lake Balkhash, and Chan (1959) has founded *Plicatomurus* for favositids from the Upper Silurian (Tiverian) of Central Kazakhstan. Sharkova (1964) has described *Scoliopora* from the 'Ludlovian' of the Tarbagatay Range.

Altai-Sayan Geosynclinal Region

This region which includes the Rudny Altai, Southern Altai, Mountainous Altai, Salair, the flanks of the Kuznetsk and Minussinsk Basins, the Sayan and Tuva, was mobile during the Siluro-Devonian, for Upper Silurian and Lower Devonian beds are missing in many places. The best-known sequences are probably those of the Altai and the Salair.

In the Salair the Baskuskan suite (including the Mt. Glyadin beds with *Mesosolenia*) is probably Wenlockian but may include basal Ludlovian. The overlying Potapov suite, with *Cantrillia* [= *Rhabdocyclus*] *eximia* Zheltonogova (1961) common, is considered Ludlovian (Nikiforova and Obut 1965). In the Altai the Chagyr suite is probably Ludlovian, and a rich fauna of Rugosa has been described by Zheltonogova (1961, 1965) and Cherepnina (1965). Tabulata (including Heliolitida and Chaetetida) have been described by Chernyshev (1951), Kraevskaya (1955a), Mironova (1961a, b, 1965), Dzyubo and Mironova (1961) and Dzyubo (1961). The Chagyr coral fauna is *Entelophyllum* [as *Stereoxyloides* and *Petrozium*], *Phaulactis microcystis* (Zheltonogova), *Ryderophyllum* Cherepnina (1965), solitary '*Neobrachyelasma balchaschia* Nik.',

'*Dokophyllum*', *Circophyllum* and '*Neobrachyelasma*' *variabile* Zhelt. [these last two are fasciculate columnariids without dissepiments and with narrow peripheral stereozone], *Tabularia oblonga* [? = *Dendrostella*], *Soshkineolites* (a homeomorph of the L. Carb. *Carcinophyllum*), *Tryplasma*, species both solitary and fasciculate [as *Zelophyllum* and possibly as *Pycnostylus*?] and *Cystiphyllum* [including '*Holmophyllum*']; *Favosites*, *Mesofavosites*, *Mesosolenia*, *Striatopora*, *Parastriatopora*, *Laceripora cribrata* Eichwald, *Taxopora altaica* Mironova, *Hillaepora*, *Heliolites tchengaensis* Mironova, *Schedohalysites pseudoorthopteroides* (Chern.), and *Halysites hamadai* Mironova. This fauna has endemic elements.

From the Gorny Altai Barskaya (1963) has described *Squameofavosites*, *Pachyfavosites*, *Heliolites pachycanaliculoides*, and *Favosites* in association with the halysitid *Hexismia*. She refers the deposits to the Upper Ludlovian, which, it seems, means Tiverian as now defined; so possibly *Hexismia* lasted into the Tiverian here, and may thus be the youngest halysitid.

In the Salair the Sukhaya suite lies between the Ludlovian Potapov suite and the Tom-Chumysh beds which are regarded by all who have worked on them as Tiverian. The corals of the Sukhaya suite that have been described by Zheltonogova (1961), Chernyshev (1951), Mironova (1960), Dzyubo and Mironova (1961) are the cerioid *Altaja? indistincta* Zhelt. (a homeomorph of *Lithostrotion* with a columella formed from a thin extension of the cardinal septum), *Dubrovina* (a solitary ptenophyllid? possibly of the *Spongophylloides perfectus* Wedekind group), *Stortophyllum*, *Squameofavosites* including *S. fungites* (Sok.), *Thamnopora khalfui* Dubatolov, *Striatopora salairica* Mironova, *Cladopora bella* Mironova, *Hillaepora spica* Mironova, *Heliolites*, and *Syringopora schmidtii* var. This suite is commonly referred to the Tiverian; perhaps it is Skalian.

The Tom-Chumysh (ostracod) beds (= Tomskozavod suite) have a brachiopod fauna regarded as equivalent to that of the Lochkov of Czechoslovakia and the Tiverian of Podolia. Its Rugosa have been described by Bulvanker (1958), Zheltonogova (1961) and its Tabulata by many: Peetz (1901); Chernyshev (1951); Mironova (1960, 1961b), Dzyubo and Mironova (1961); Dubatolov (1959, 1963); Dubatolov and Chekhovich (1964), and Chudinova (1959, 1964).

Its rugosan fauna comprises *Phanlactis cyathophylloides* Ryder of Bulvanker, and '*Pilophyllum*' *insolitum* Zhelt. (both probably cyathophyllids like *Radiophyllum*), *Pilophyllum angustum* Zhelt. (possibly ptenophyllid), and *Dubrovina* also possibly ptenophyllid, the spongophyllids *Spongophyllum shearsbyi*? Chapman, cerioid *Neomiphyina rosiformis* Zhelt. and tryplasmids, solitary and fasciculate. Of the Tabulata, *Squameofavosites* has the most numerous species, but species of *Dictyofavosites* (the first), *Favosites*, *Pachyfavosites*, *Striatopora*, *Parastriatopora*, *Thamnopora*, *Heliolites*, *Pachycanalicula*, and *Syringopora* are also characteristic. Dubatolov (1959) listed, as *Multisolenia*, *Palaeofavosites mirabilis* var. *baskuskanensis* Cherny. (1951). This may represent the youngest occurrence of *Multisolenia*. With these beds are correlated the Lochtev limestones of the Altai (Dubatolov 1962, Dubatolov and Chekhovich 1964) with *Favosites kogulaensis* (which is Lower Ludlow in Estonia), *Squameofavosites*, and *Parastriatopora*.

Siberian Platform

On the Siberian platform upper Silurian deposits are confined to the north-west flank of the Tungus syncline and the south flank of the Anabar antecline. *Parastriatopora*

and *Favosites* ex gr. *coreaniformis* occur (Sokolov and Tesakov 1963, Nikiforova and Obut 1965) and may be Ludlovian.

North-eastern U.S.S.R.

In the Verkhoyan–Chukotsk geosyncline of north-eastern U.S.S.R. Ivanovskiy (1965b) refers to Ludlovian *Lamprophyllum* from the R. Kolyma. The Tiverian? Nelyudum suite in the Ormulev Mountains in the basins of the R. Kolyma and R. Tirekhtya has abundant *Favosites socialis* Sokolov and Tesakov (1963) and new species of *Favosites*. Nikiforova and Obut (1965) refer to Tiverian beds with *Favosites* ex gr. *coreaniformis* Sok. and *Squameofavosites* in the basins of the Rivers Ormulev and Taskar, and beds with *F.* aff. *coreaniformis*, *Favosites*, and *Dictyofavosites* in the Sette-Daban Range. *F. socialis* occurs also in the Tiverian of the R. Pechora and the northern Urals. Earlier descriptions are by Chernyshev (1936, 1941b), Rukhin (1938b), and Nikolaeva (1936).

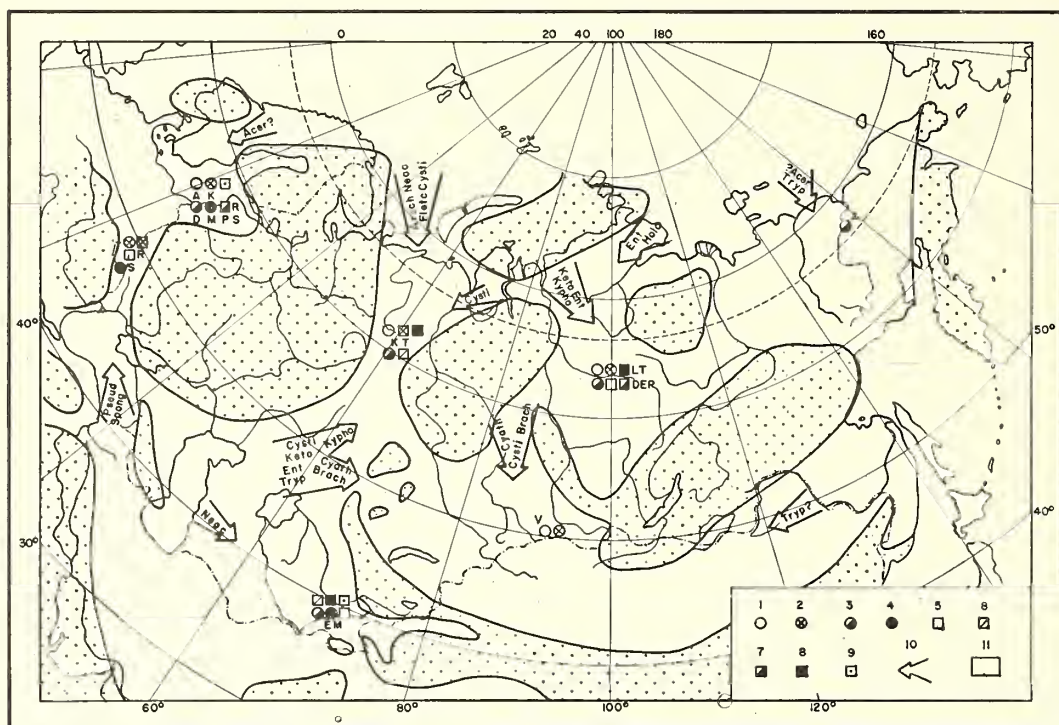
Faunal Analysis and Palaeozoogeography

Sokolov, Kovalevskiy, and Chekhovich (in Nikiforova and Obut 1965) state that the Ludlovian and Tiverian tabulatan faunas of the U.S.S.R. might be considered as forming one zoogeographic province and that regional differences are most likely due to facies. A similar opinion regarding the rugosan faunas is held by Kal'o (1965), who considered that in the pre-Ludlovian Silurian, two provinces were distinguishable, the European–central Asiatic, and the Siberian–American and that the degree of faunistic difference gradually decreased. Kal'o's map of the Wenlockian seas of the U.S.S.R. showing his suggested migration routes of the Rugosa is given in text-fig. 1.

Analysing the foregoing, we may say that the Ludlovian is characterized by genera with few exceptions (e.g. *Weissermelia*) relict from the Wenlockian, and consists nearly everywhere mainly of the Rugosa *Phaulactis*, *Entelophyllum*, *Weissermelia*, *Pilophyllum*, *Spongophylloides* of the *perfectus* (Wdkd.) group which are morphologically close to *Acanthophyllum*, numerous solitary and phaceloid tryplasmids, *Cystiphyllum*, *Holmophyllum*, and *Rhizophyllum*, with the Tabulata *Favosites*, *Palaeofavosites*, *Multisolenia*, *Parastriatopora*, *Alveolites*, *Coenites*, *Thecia*, *Laceripora* (the last?), *Heliolites*, *Propora*, *Halysites* (the last), *Aulopora*, and *Syringopora* and *Romingerella* (the first). In the Tien Shan *Squameofavosites* is recorded in an early occurrence, and in the Altai-Sayan, *Hillaepora*. Halysitids are not recorded from younger strata, except for *Hexismia* sp. from the 'Upper Ludlow' (i.e. presumably Tiverian) of the Mountainous Altai. Sokolov (1962d) concluded that for the wider correlation of Ludlovian (s.s.) deposits, of leading significance are *Favosites* ex gr. *forbesi*, *Thecia swinderniana*, *Mesolenia festivus*, and *Helioplasmodites* amongst others.

A small fauna distinguished in some regions and following this one includes, like the Skalian, '*Dokophyllum*', *Spongophylloides*, ?*Acanthophyllum*, solitary and fasciculate tryplasmids, species referred to *Holmophyllum* but some probably not of that genus, and *Cystiphyllum*. *Phaulactis* and *Weissermelia* are recorded but not illustrated. *Favosites* is predominant but rare *Squameofavosites* occur and *Thamnopora* with rare *Multisolenia* (the last?). *Thecostegites* enters in beds that may be Skalian in the Polar and Sub-polar Urals, with the Rugosan *Scyphophyllum* Strel'nikov. This fauna is not very different from that of the Ludlovian, with the possible exception that *Thecostegites* and *Thamnopora* (s.s.) have entered.

Nikiforova and Obut (1965) consider that in the early Ludlow regression of the seas began, reaching its maximum in Tiverian time, when, however, migration was still possible from Podolia via the Urals and South Caucasus to Central Asia. Their map is redrawn in text-fig. 2.



TEXT-FIG. 1. Directions of migration and geographical distribution of Wenlockian Rugosa.

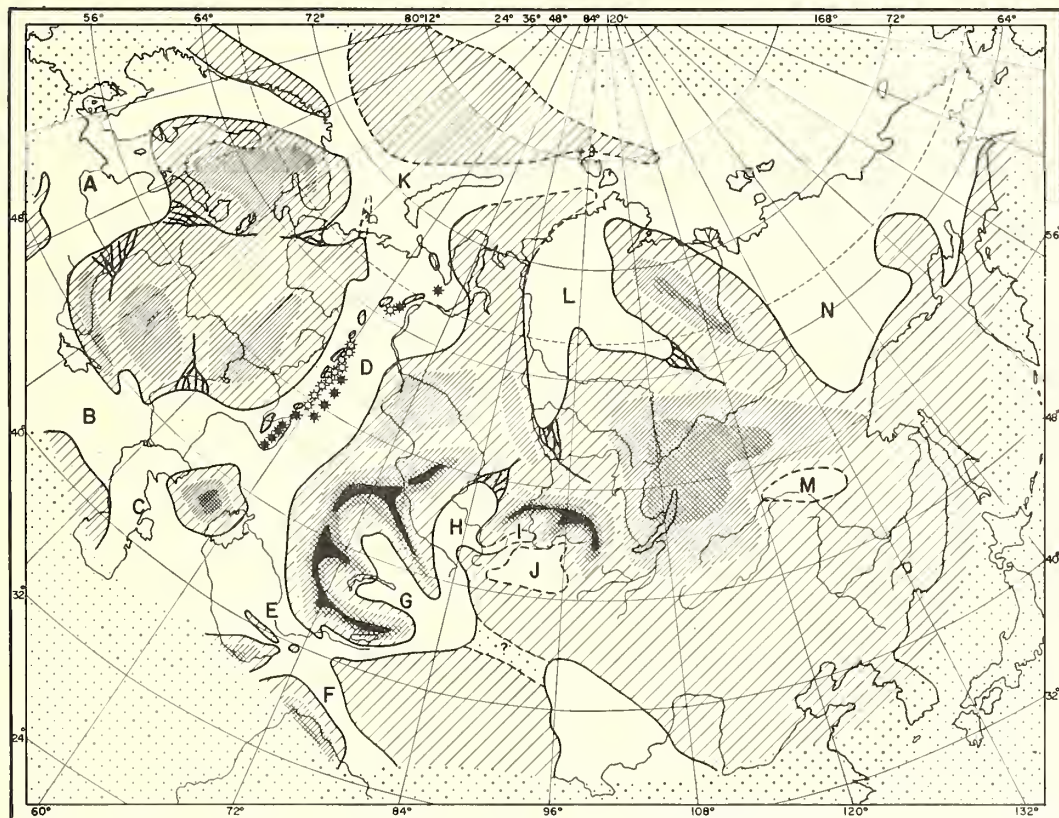
1, *Hedstromophyllum*; 2, 'Microplasma'; 3, *Neocystiphyllum*; 4, *Phanlactis*; 5, *Cyathactis*; 6, *Holmophyllum*; 7, *Kyphophyllum*; 8, *Micula*; 9, *Zelophyllum*; 10, probable direction for the genera named in the arrow.

Acer (A), *Acervularia*; Arach, *Arachnophyllum*; Brach, *Brachyelasma*; Cyath, *Cyathactis*; Cysti, *Cystiphyllum*; D, *Dentilasma*; E, *Dinophyllum*; Ent, *Entelophyllum*; Fletc, *Fletcheria*; Keto, *Ketophyllum*; K, *Kodonophyllum*; Kyph, *Kyphophyllum*; L, *Lamprophyllum*; Neoc, *Neocystiphyllum*; Pseud (M), *Pseudamplexus*; P, *Pycnactis*; R, *Rhizophyllum*; Spong, *Spongophylloides*; S, *Spongophyllum*; T, *Tabularia*; Tryp, *Tryplasma*.

I, Prebaltic; II, Podolia; III, Tadzhikistan; IV, Urals; V, Sayano-Altai; VI, Siberian platform; VII, NE. U.S.S.R. After Kal'ov, 1965.

Tiverian faunas are sometimes divisible into two, but these taken together comprise *Neobrachiylasma* Nik., *Palaeocyathus* Foerste (= *Orthopaterophyllum* Nik.), 'Diplophyllum' (a disphyllid?), *Spongophylloides* of the *perfectus* Wdkd. group, 'Fasciphyllum' and numerous solitary tryplasmids and cystiphyllids, with *Favosites*, *Pachyfavosites* (the first?), *Squameofavosites*, *Dictyofavosites* (the first), *Multisolenia* (the last?), *Cladopora*, *Hillaepora*, *Thamnopora*, *Striatopora*, *Parastriatopora*, *Heliolites*, *Propora*, *Pseudoplasinopora*, *Squameolites*, *Syringopora*, and *Thecostegites*.

The boundary between the Silurian and Devonian seems to me to be possibly best taken at the base of the Tiverian and the base of the Lochkovian and the base of the Gedinnian, all of which appear in the continuing results of the Prague and Bonn symposia to represent practically the same point in time, which may well be part of Ludlow Bone Bed time, or perhaps the base of the Downtonian.



TEXT-FIG. 2. Tiverian Geography of Eurasia.

A, Palaeo-Baltic Sea; B, South European Sea; D, Ural Sea with volcanoes; E, Tien Shan Sea; F, Tadzhik Sea; G, Balkhash-Karaganda Sea; H, Altai Sea; I, Sayan Gulf; J, Tuva-Mongolian remnant basin; K, Novozemel Sea; L, Tungus Sea; M, Amur remnant basin; N, Verkhoyan Sea. Dotted area unknown or not analysed. Contouring of land is indicated by closeness of lining and mouths of rivers are shown. After Nikiforova and Obut, 1965.

The value of the Tabulata as indicators of the boundary between Silurian and Devonian has been argued by Mironova (1961*b*) on the one hand and by Dubatolov and Chekhovich (1964) on the other. Thus Dubatolov and Chekhovich consider that a sharper palaeontological boundary may be fixed in the Kuznetsk Basin, in Central Asia, and in Podolia at the top of the Tiverian and the base of the Krekov by the complete disappearance above this boundary of the genera *Palaeofavosites*, *Mesofavosites*, *Syringolites*, and *Propora* and by the appearance above it of *Pseudoroemeria*, *Roemeripora*, *Dendropora*, *Crassialveolites*, *Placocoenites*, and *Lecomptia*. Mironova noted that

the extinction of the halysitids and the multisolenids and the incoming in force of *Pachyfavosites*, *Dictyofavosites*, *Squameofavosites*, and *Thecostegites* gave a sharpness to the base of the Tiverian; however, rare exceptions occur, as noted above.

Both boundaries appear to have value in correlations within Eurasia, and may well be applicable elsewhere, regardless of where it is finally decided to draw the Silurian-Devonian boundary.

It should be noted that the only ptenophyllids figured from Tiverian strata are solitary corals referable to the *Spongophylloides perfectus* (Wdkd.) group of species which was present in the Ludlovian (and which may be *Acanthophyllum s.l.*) and the fasciculate '*Fasciphyllum*' *kokshalicum* Pavlova. There is a notable absence of *Xystriphyllum* and *Taimyrophyllum* as also of disphyllids (solitary, fasciculate, cerioid, and thamnastraeoid) and of *Pseudamplexus altaicus* (Dybowski).

It seems that the 'Upper Ludlovian' or 'Tiverian' of Asiatic Russia is broadly equivalent to the Lochkovian but the base and top of the faunal interval have still to be determined in the different regions. The equivalence of the Asiatic Tiverian with the stratotype Tiverian in Podolia is not yet certain either. If the Czortkow fishes are lower Gedinnian, as Tarlo thinks, the type Tiverian may be older than much of the Asiatic 'Tiverian'.

POST-TIVERIAN AND PRE-COUVINIAN

These are the faunas thought by this reviewer to be equivalent to the Pragian and Zlichovian of Czechoslovakia and to the upper Siegenian and Emsian of western Europe. None are described from Podolia.

Novaya Zemlya

A Lower Devonian assemblage from the horizon of the Morzhov Inlet has recently been described, the Rugosa by Kravtsov (1965) and the Tabulata by Smirnova (1965b). It consists of *Pseudamplexus altaicus* (Dyb.), *Acanthophyllum*, *Spongophyllum* [?] (solitary? or phaceloid), *Tryplasma*, *Stortophyllum* [?] and *Plasmophyllum* (*Plasmophyllum*) (as *Cystiphyllodes*, *Nardophyllum*, and *Pseudomicroplasma*); and of *Favosites*, *Squameofavosites*, *Dictyofavosites*, *Syringolites* (?), *Pachyfavosites*, *Striatopora*, *Thannopora*, *Caliapora*, *Alveolites*, *Alveolitella*, and *Syringopora*.

Urals

Soshkina (1937, 1941, 1949a, b, 1951, 1952), Spasskiy (1959), and Pavlova (1956) have described Lower Devonian Rugosa from the eastern and western slopes of the Urals and Porfir'ev (1937), Sokolov (1952b), and Yanet (1956, 1965) have described Tabulata. Chernyshev (1885, 1887, 1893) included descriptions of corals in his faunal papers. Some of the ages assigned in the early works have been modified in the later papers.

Correlation of the widely spread strata is still in progress and at present it does not seem that they can be precisely apportioned to the west European stages. The faunal lists of Spasskiy (1964) and Dubatolov (1964) have presumably taken account of increasing stratigraphic knowledge along the Urals, but unfortunately they do not enable me to refer precisely to the relevant illustrations of species. Spasskiy (1959) states that the following species have maximum distribution in the lower part of his post-Tiverian Lower Devonian of the eastern slopes (upper part of the Petropavlovsk formation):

Pseudamplexus quadripartitus (Soshk.), 'Acanthophyllum heterophyllum E. & H.' and *Fasciphyllum petschoreuse* Soshk. These he called Gedinnian. The 'Coblentzian' beds with *Karpinskia conjugula* contain *Pseudamplexus* (solitary and weakly colonial species), *Chlamydoephyllum tabulatum* (Soshk.), cerioid *Favistella minor* (Soshk.) and *F. massivum*, *Lyrielasma petschoreuse* (Soshk.) (these last two species at the top), *Neophyma originata* and *N. striata* S., *Acanthophyllum*, *Australophyllum*? (as *F. petschoreuse* pars.), *Xystriphyllum medianum* (S.), *Tainyrophyllum*, *Spongophyllum halysitoides*, *Tryplasma*, *Plasmodiophyllum* (*Plasmophyllum*) as *Pseudomicroplasma* and large *Rhizophyllum* occur; also *Favosites*, *Squameofavosites*, *Parastriatopora*, the *Cleistopora*-like *Rhiphaeolites* Yanet 1956, and *Syringopora*.

Central Asia

In the ranges of Turkestan, Gissar, Fergana, Alay, Nuratau, Kokschaaltau, and in the Pamir and Darwas, the post-Tiverian Lower Devonian Akkul suite contains numerous *Pseudamplexus* including *P. altaicus* (Dyb.) and *Acanthophyllum*, together with *Chlamydoephyllum tabulatum* (Soshk.), *Neophyma striata* Soshk., *Loyolophyllum*, *Spongophyllum halysitoides* Eth., fasciculate *Tryplasma* (as *Aphyllum*), *Rhizophyllum enorme*, and *Plasmodiophyllum* (*Plasmophyllum*) [as *Pseudomicroplasma*]. See Goryanov *et al.* (1961) and Spasskiy (1964). From the Dzhdalin suite of the Lower Devonian of S. Fergana Pavlova (1963, 1965) included in *Fasciphyllum* two cerioid species that could be *Xystriphyllum* and from the Akkul suite *Xystriphyllum prismaticum* (Soshk.) (see also Goryanov, 1962, 1963).

Dubatolov (1964) and Dubatolov and Chekhovich (1964) listed tabulatan species determined by Chekhovich but not yet illustrated from the Manak suite of Central Asia as of the genera *Favosites*, *Oculipora*, *Dictyofavosites*, *Squameofavosites*, *Pachyfavosites*, *Parastriatopora*, *Striatopora*, *Cladopora*, *Pseudoroemeria* Chekhovich (1960), *Helioplasma*, and *Heliolites*.

Leleshus (1964b) has described from Lower Devonian 'Coblentzian' beds with *Karpinskia conjugula* from the northern slopes of the Zeravshan Range, the new tabulatan genus *Rudakites*, like *Thamnopora* but with intermural increase. Listed with it are *Favosites*, *Squameofavosites*, *Dictyofavosites*, *Emmonsia*, *Pleurodictyum*, *Striatopora*, and *Crassialveolites* and the Rugosa *Pseudamplexus*, *Lyrielasma petschoreuse* (Soshk.), *Spongophyllum halysitoides* Erh., *Tryplasma*, and *Rhizophyllum enorme* Eth.

Goryanov (1963) considers that in the Southern Tien Shan the Lower Devonian fauna is not divisible into zones but is analogous to the Pragian of Czechoslovakia. He lists *Chlamydoephyllum tabulatum* (Soshk.), *Lindstroemia* spp., *Petraia* spp., *Syringaxon* spp., *Barrandeophyllum*, *Oligophyllum*, *Orthopaterophyllum* [= *Palaeocyathus*], *Pseudamplexus* [as *Mucophyllum*] and *P. altaicus*, *Kionelasma* spp., *Kodonophyllum* spp., *Desmiophyllum*, 'Eutelophyllum', *Pilophyllum*, *Acanthophyllum* spp., *Ptenophyllum* spp., *Spongophyllum halysitoides* Etheridge, *Loyolophyllum cresswelli* Chapman, *Fasciphyllum halliaforme*, *Lyrielasma ?petschoreuse* (Soshk.), *Xystriphyllum prismaticum* (Soshk.), *Aphyllum*, *Tabularia*, *Tryplasma*, cystiphylloids (under the names *Pseudomicroplasma*, *Wedekindophyllum*, and *Pseudodigonophyllum*), and *Rhizophyllum enorme* Eth.

Kazakhstan

Spasskiy (1965) described from rocks of the Dzhungarian Alatau which he ascribed to the Gedinnian but which may be Pragian, the new genus *Neokyphophyllum* [resembling

Pilophyllum] and listed *Orthopaterophyllum* [= *Palaeocyathus*], *Tryplasma devonianum* (Soshk.), *Tabularia*, *Favosites*, and *Heliolites*. As Coblenzian he listed *Barrandeophyllum*, *Orthopaterophyllum*, *Chlamydothyllum*, *Pseudamplexus*, and *Acanthophyllum*. From the northern sub-Balkash he listed (1964) *Xystriphyllum devonicum* (Bulv.). Sokolov (1962d) reported that Tabulata here and in some districts of Central Asia and parts of the Mongolo-Okhotsk geosyncline are rare and usually represented by *Pleurodictyum* and rare *Thamnopora* and *Trachypora*.

Altai-Sayan Geosynclinal Region

For this coral-rich region, the coral faunal sequences of the south-western margins of the Kuz Basin and the northern Salair may be taken herein as the standard of reference; the stratigraphic sequences in other parts of the region differ, but some suggested correlations are mentioned.

As seen above, the Tom-Chumysh beds are, by correlation with the *Monograptus hercynicus*-bearing *marginalis* beds of the Kunzhak suite of the Zeravshan Range, to be regarded as Lochkovian (i.e. within the range Gedinnian to base of early Upper Siegenian). Above them lie the Krekov beds.

The rugosan fauna of the Krekov beds has been described by Kraevskaya (1955b), Bulvanker (1958), Ivaniya (1957a, b; 1958a, b, c, d; 1960; 1961), and Zheltonogova and Ivaniya (1961) and consists of *Syringaxon*, *Petrozium* [?], *Pseudamplexus altaicus* (Dyb.) *Pseudotryplasma* Ivaniya (like *P. altaicus* but with sporadic large dissepiments), *Dendrostella columnaris* Zhelt. (as *Soshkinella*), *Tryplasma sociale* (Soshk.), *Plasmophyllum* (*Plasmophyllum*) [as *Pseudomicroplasma* and *Diplochone*], *Rhizophyllum gervillei* Bayle, and *R. enorme* Eth. See also Ivaniya (1965).

Tabulata of the Krekov beds have been described by Peetz (1901), Chernyshev (1951), Kraevskaya (1955a), Chudinova (1959, 1964), Dubatolov (1956, 1959, 1963, 1964), Dubatolov and Mironova (1961a, b, c), Dubatolov and Chekhovich (1964), Dubatolov and Smirnova (1964), and Mironova (1957, 1961a, b, c), and discussed by Khalfina (1956). *Favosites*, *Dictyofavosites*, *Squameofavosites*, rare *Pachyfavosites*, *Syringolites*? (last appearance?), *Parastriatopora*, *Thamnopora*, *Striatopora*, *Gracilopora* (first appearance), *Cladopora*, *Dendropora*, *Crassialveolites* (first appearance), *Coenites*, *Placocoenites*, *Leocomptia*, *Stelliporella*, *Heliolites*, *Pachycanalicula* (first appearance), *Syringopora*, and *Roemeripora* (first appearance) all occur. The first three genera named above are dominant.

The Malobachat beds with *Karpinskia conjugula* Tschernychev overlying the Krekov beds have Rugosa described mainly by Kraevskaya (1955b) and by Zheltonogova and Ivaniya (1961): *Syringaxon*, *Pseudamplexus altaicus* (Dyb.), the solitary disphyllid *Gurievskiella* Zhelt., *Neomphyma*, *Acanthophyllum* (as *Pseudochonophyllum*), *Lyrielasma*, *Xystriphyllum gorskii* (Bulv.), *Taimyrophyllum*, and *Tryplasma*. Tabulata, described in the same works as those of the Krekov beds are *Favosites*, *Pachyfavosites*, *Striatopora*, *Cladopora*, *Alveolites*, *Heliolites*, and *Syringopora* and for the most part the species are different from those of the Krekov beds. Bulvanker (1958) referred to the rugosan genus *Loyolophyllum*, a species (*brevisseptata*) of the tabulatan *Roemeripora*. The transverse section she figured shows mural pores. Kraevskaya (1955b) referred to the undifferentiated Lower Devonian two cerioid small-celled *Spongophyllum* spp. See Ivaniya (1965).

Similar tabulatan faunas to those of the Krekov and Malobachat beds have been

described from the Mountainous Altai (Cherepnina and Dzyubo 1962, Dubatolov 1964).

Taimyr

Lower Devonian Rugosa and Tabulata of the Taimyr have been described by Chernyshev (1941a), Lower Devonian Rugosa by Kravtsov (1963) and Lower Devonian Tabulata by Dubatolov and Smirnova (1964) and Smirnova (1965a). Lists of species have been given by Spasskiy (1964), Dubatolov (1964), Smirnova (1965 a, c), and Kravtsov and Smirnova (1965).

The lowest of three post-Tiverian Lower Devonian coral faunas contains *Squameofavosites*, *Parastriatopora*, and *Striatopora*. The second has *Pseudamplexus altaicus* (Dyb.), *Tryplasma devonianum* (Soshk.), *Plasmophyllum* (*Plasmophyllum*) [as *Pseudomicroplasma* and *Zonophyllum* spp.], *Tabularia* [?], *Zmeinogorskia* [= *Heterophentis*?], *Anlacophyllum* [?], *Taimyrophyllum speciosum* Chernyshev and presumably also *Disphyllum? planivesiculosum* (Chern.) together with *Favosites kolymensis* Chern. and *F. spp.*, *Squameofavosites*, *Parastriatopora*, *Striatopora*, *Caliapora*, *Pleurodictyum?*, and *Syringopora*. The highest has *Tryplasma devonianum* (Soshk.), *Plasmophyllum* (*Plasmophyllum*) [as *Pseudozonophyllum*] and *Xystriphyllum taimyricum* (Kravtsov), with *Squameofavosites*, *Thamnopora taimyrica* (Chern.), and *Alveolitella* (first appearance).

Transbaikalia and the Mongolo-Okhotsk (Amur) Geosyncline

In the Upper Amur, the Bolshenev suite is considered Lower Devonian, possibly later Lower Devonian. Spasskiy (1960b) described *Barrandeophyllum perplexum* Poeta and *Lindstroemia minima*; Dubatolov (1964) listed *Favosites* and *Pleurodictyum*. The younger Imachin suite, possibly ranging from the late Lower into the Middle Devonian (Dubatolov 1964) or possibly entirely Eifelian (Spasskiy 1960b, 1964), contains 'Zaphrentis', *Plasmophyllum* (*Plasmophyllum*) [as *Pseudomicroplasma* and *Lythophyllum*] and *Cyathophyllum* (*Peripaedium*) *spinulosum* (Soshk.). This latter species seems from Spasskiy's figures to differ from Soshkina's type and to be a cyathophyllid quite close to *Radiophyllum arborescens* Hill from the Emsian? Mt. Etna limestone of Queensland. Tabulata are *Favosites*, *Squameofavosites*, *Crenulipora*, *Thamnopora*, and *Tyrganolites*—this last genus normally being an indicator of Middle Devonian.

The Lower Devonian Il'dikan suite of eastern Transbaikalia contains *Favosites* and *Striatopora* (Dubatolov 1964) and, near the Gazimov works, *Barrandeophyllum*, *Tabulophyllum* [?] sp., *Pseudamplexus fascicularis* (Soshk.) *Favistella*, and the endemic, solitary *Gazimria ildicanica* Spasskiy (1960b). Spasskiy (1964) suggests that the upper part of the Il'dikan suite contains 'Stenophyllum' sp. The Blagodat suite around Nerchin contains *Lindstroemia minima* Spasskiy (1960b), *Favosites*, *Parastriatopora*, *Alveolitella*, and *Placocoenites* (Rukhin 1936, Dubatolov 1964).

North-eastern U.S.S.R.

From the upper part of the Upper Silurian of the R. Kolyma, Rukhin (1938b) has established *Kozłowiaphyllum* which Ivanovskiy (1965b) has considered a synonym of *Temniphyllum* Soshkina and regarded as Wenlockian. From the Lower Devonian, Rukhin described *Entelophylloides inequalis* (Hall) which is possibly the same genus as *Xystriphyllum*. Bulvanker (1965) figured from the undivided Lower Devonian of the

Ormulev region *Acanthophyllum mansfieldense* (Dun), *Taimyrophyllum colymense* Bulv., *Pseudamplexus altaicus* (Dyb.), and *Plasmophyllum* (*Plasmophyllum*) aff. *nesterowskii* (Peetz). From beds regarded as transitional from Lower Devonian to Eifelian she figured *Acanthophyllum* spp., *Taimyrophyllum carinatum* Bulv., and *P. altaicus*. Other descriptions are by Bulvanker (1948). Spasskiy (1964) listed *Tryplasma maximum* (Chern.) additionally in a similar fauna from the Verkhoyan.

Tabulata have been described by Chernyshev (1936), Rukhin (1938b), and Dubatolov and Spasskiy (1964b) and Dubatolov (1964) has supplied lists of Lower Devonian forms. The distinctive feature of the north-east Siberian fauna is the presence of *Favosites socialis* Sok. and Tes. and of great numbers of local species of *Parastriatopora*, *Striatopora*, *Cladopora*, *Alveolitella* and *Caliapora*, the endemic *Yacutipora* (like *Parastriatopora* but with trabecular wall thickening in the peripheral part of the branch, and long narrow pore canals with diaphragms), and the absence of heliolitids. *Dictyofavosites* and *Squameofavosites* occur also in the Sette-Daban and Tas Khayakhtakh regions.

Faunal Analysis and Palaeozoogeography

Reviewing the above, we see that the Altai-Sayan faunas are the best illustrated and further that in the Salair there is a proved sequence of faunas from that of the Tom-Chumysh beds, through the Krekov beds and into the Malobachat beds. If we accept the correlation of the Tom-Chumysh beds with the Kunzhak beds of the Zeravshan Range in the Tien Shan, as indeed seems completely reasonable, we then have the probability that the Tom-Chumysh beds are Upper Lochkovian, since *Monograptus hercynicus*, *Paranowakia geinitziana* Bouček and *P. obuti* Bouček are reported from the Kunzhak beds, though I have found no illustrations to substantiate the identifications. The Krekov beds may then well be Pragian, within the range Upper Siegenian–Lower Emsian and the Malobachat beds may possibly be either Lower Emsian or Zlichovian. Such correlations can be only very tentative at present.

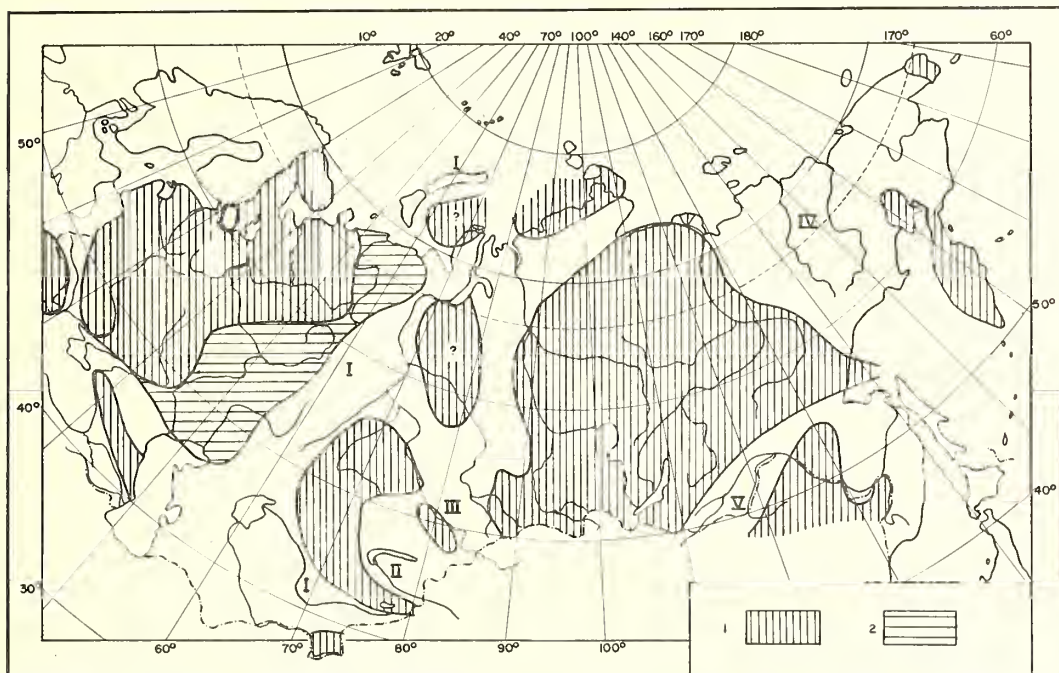
The Krekov fauna as listed above, is very similar to the Pragian upper Konieprus fauna of Czechoslovakia, differing mainly in the absence of ptenophyllids, but ptenophyllids are found in force accompanying *Pseudamplexus altaicus* and tryplasmids, *Rhizophyllum enorme* and *Roemeripora* in the overlying Malobachat beds, where '*Pseudochonophyllum*', phaceloid *Neomphyma*, cerioid *Xystriphyllum*, and thamnastreaeid *Taimyrophyllum* occur (Zheltonogova and Ivaniya 1961), together with *Spongophyllum halysitoides* Eth. and the solitary disphyllid *Gurievskiella* Zhelt. We are left wondering whether the absence of ptenophyllids and disphyllids in the Krekov beds and their presence in the overlying Malobachat beds is due solely to the difference in age.

The Krekov plus Malobachat beds and their correlatives in Asia are clearly distinguished from the underlying Tiverian by an assemblage of the Rugosa *Pseudamplexus* (especially *altaicus*), †*Gurievskiella*, †*Loyolophyllum*, †*Neomphyma*, *Acanthophyllum* (s.l.), †*Lyriellasma*, †*Xystriphyllum*, †*Taimyrophyllum*, *Spongophyllum*, *Tryplasma*, *Plasmophyllum* (*Plasmophyllum*) and *Rhizophyllum*, together with the Tabulata *Favosites*, *Dictyofavosites*, *Squameofavosites*, *Pachyfavosites*, *Thamniopora*, †*Gracilopora*, and †*Roemeripora*. The genera marked † are not known in older beds in Asia.

The chief character of the tabulatan fauna is the exceptionally wide and rich development of the squamulate favositids *Squameofavosites* and *Dictyofavosites*, many of the species having profuse mural pores; also notable is the wall thickening of the branching

favositids *Parastriatopora* and *Striatopora*; the *Thamnopora* and *Cladopora* species have relatively thin walls, and the heliolitids show some thickening of the walls of their interstitial tubuli; at the same time the alveolitids differ from Silurian representatives in the thickening of their walls.

Dubatolov's (1964) and Spasskiy's (1964) maps, here reproduced as text-figs. 3 and 4, show their views on the zoogeographic provinces of the Lower and Middle Devonian, Spasskiy's map showing also the reefs and his deduction on the position of the equator.



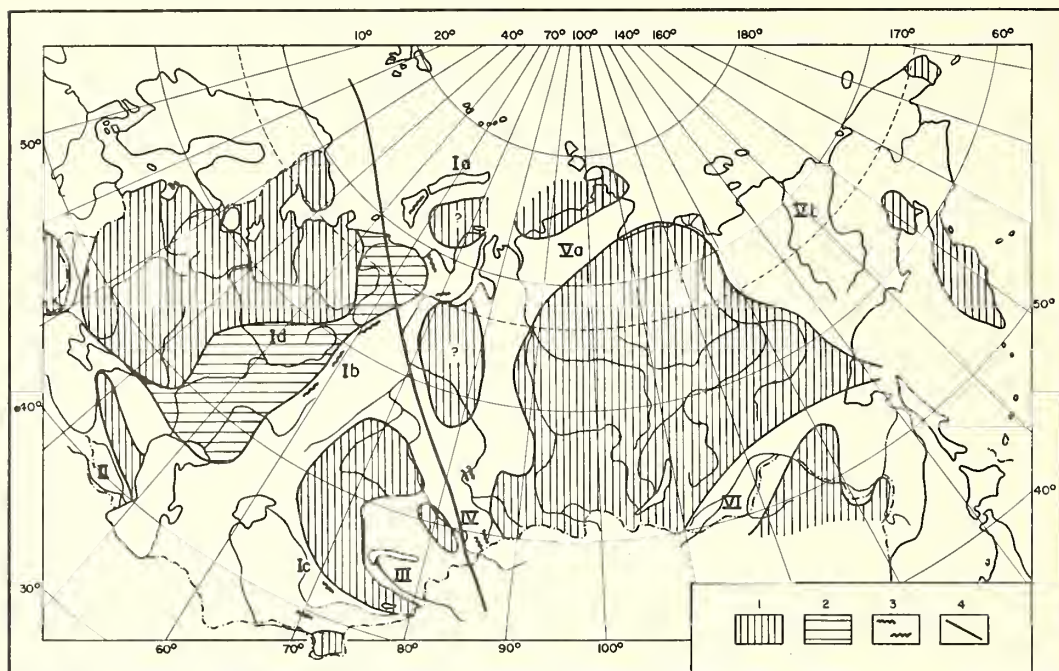
TEXT-FIG. 3. Palaeozoogeographic provinces in the Early and Middle Devonian, based mainly on the Tabulata.

1, land; 2, epicontinental sea. Provinces: I, Uralo-Tien Shan; II, Dzhungaro-Balkhash; III, Altai-Sayan; IV, Indigiro-Kolyma; V, Mongolo-Okhotsk. After Dubatolov, 1964.

In my view, however, the distribution of the reefs can be equally well explained by climatic and temperature difference induced by the Devonian relation of continents and oceans, with the continental nuclei in their present position relative to the poles and to the present direction of the axis of rotation of the earth.

The Uralo-Tien Shan Province including Novaya Zemlya and the Taimyr with *Pseudamplexus*, *Chlanydophyllum*, *Tryplasma*, *Acanthophyllum*, and *Favosites* dominant, and with *Striatopora* and *Cladopora* present is considered continuous with that of Western Europe via Asia Minor and the Mediterranean region. The Altai-Sayan Province is characterized by *Tryplasma*, *Acanthophyllum*, and in the younger beds by ptenophyllids, and by the dominance of *Squameofavosites*, *Dictyofavosites*, and *Plicatomurus*, and the presence of *Cleistopora*, *Placocoenites*, and *Lecomptia*. The Dzhungarian-Balkhash province has, as known at present, only small solitary non-

disseminated Rugosa (due to facies?); the Tabulata, though also poorly known, suggest to Dubatolov (1964) sharp regional differentiation. The Mongolo–Okhotsk province appears characterized by the absence of *Tryplasma*, *Acanthophyllum*, *Striatopora*, *Thamnopora*, *Cladopora*, *Alveolites*, and *Heliolites*, and the presence of distinctive species of *Pleurodictyum*, *Favosites*, and *Sqnameofavosites*. The Indigiro–Kolyma Province



TEXT-FIG. 4. Palaeozoogeographic provinces in the Early and Middle Devonian, based mainly on the Rugosa.

1, land; 2, epicontinental sea; 3, hercynian reefs; 4, position of the equator suggested by Spasskiy. Provinces: I, Uralo–Tien Shan; a, Pay–Khoy–Novozemel region; b, Ural region; c, Central–Asian region; d, Volgo–Timan region. II, Caucasus region of the Mediterranean province. III, Dzhungaro–Balkhash. IV, Altai–Sayan. V, Indigiro–Kolyma; a, Taymyr region; b, Kolyma region. VI, Mongolo–Okhotsk. After Spasskiy, 1965.

shares a rugosan complex with the Taimyr region—*Taimyrophyllum speciosum* and *Tryplasma maximum* being characteristic; its tabulatan fauna is distinct, characterized by an abundance of branching *Favosites* ex gr. *socialis* and the endemic *Yacutipora*.

COUVINIAN

Russian formations and faunal horizons referred to the 'Eifelian' have been so referred by general faunal correlation. According to Sokolov (1962d) the common usage of 'Eifelian' in the U.S.S.R. includes the Eifelian proper and the *cultrijugatus* beds, and is thus presumably equivalent to the Couvinian of Belgian geologists. They lie below *Stringocephalus*-bearing beds referred to the Givetian, contain *Conchidiella* in the greater, upper part and, in some regions, *Paraspirifer* in the lower part and lie above beds

bearing *Karpinskia conjugula* which have been generally referred to the Coblenzian, but which in her review of Devonian correlations Rzhonsnitskaya (1962) has called Lower Emsian and Upper Pragian.

In the same review Rzhonsnitskaya has referred the *Paraspirifer* beds (= zone of *Favosites regularissimus* of the eastern slopes of the Urals and the Salairkin beds of the Kuznetsk sequence) to the Zlichovian which she accepted as Upper Emsian but regarded as equal to the Assise de Bure of Belgium and considered Middle Devonian but pre-Eifelian. However, in most current Russian work the east Uralian zone of *F. regularissimus* and the Salairkin beds are called Lower Eifelian.

Unfortunately the Russian zonal brachiopods do not occur in Western Europe, but detailed work on brachiopod groups such as the Atrypida, as well as on the goniatites, conodonts, tentaculites, and corals now in progress must eventually give precise correlations both within the U.S.S.R. and with the standard sequences of Western Europe. In the meantime we must regard the Salairkin beds and their correlates as possibly Upper Emsian or possibly Lower Couvinian.

Novaya Zemlya, Vaygach Island, and Pay-Khoy

Spasskiy (1964) and Dubatolov (1964) listed from the 'early Eifelian' of this northern region *Barrandeophyllum*, *Pseudamplexus*, *Chlamydoephyllum* (as *Zelophyllia*), *Loyolophyllum*, *Neocolumnaria vagranensis* Soshk., *Spongophyllum halysitoides* Eth., *Acanthophyllum*, *Neomphyma striata* Soshk., *Fasciphyllum orientale* Soshk., *Xystriphyllum muralicum* (Soshk.), *Tryplasma* and *Plasmophyllum* (*Plasmophyllum*) [as *Pseudomicroplasma*], and the Tabulata *Favosites regularissimus* and *Pachyfavosites*.

From the later Eifelian Spasskiy (1964) listed *Zelophyllia*, *Cyathophyllum* (*Peripaedium*) *spinulosum* (Soshk.), '*Campophyllum*' *soeticum* Schlüter, '*Charactophyllum*' *antiquum* Soshkina, *Favistella floriformis* (Soshk.), *Neomphyma striata*, *Tryplasma*, *Plasmophyllum* (*Plasmophyllum*) [as *Lythophyllum*, *Zonophyllum*, *Pseudozonophyllum*], *P. (Mesophyllum)* [as *Digonophyllum*] and *Calceola*. Dubatolov (1964) listed *Favosites* ex gr. *goldfussi* d'Orb. and *Syringopora eifeliensis* Schlüter. Descriptive papers are scanty (Chernyshev 1937a, 1938a, b).

Urals

The 'Eifelian' of the western slopes of the Urals, earlier taken to comprise the Takatin, Vanyashkin, and Vyazov beds and their correlatives has been augmented by the overlying *Calceola* and Biya beds which were removed from the Givetian by resolution of a conference held in Sverdlovsk in 1957 (Spasskiy 1960a). Similarly the 'Eifelian' of the eastern slopes has been augmented (Spasskiy 1959; Khodalevich *et al.* 1959) by the highest of the beds with *Conchidiella bashkirica* (D₂ 2a and D₂ 2b of Andronov) previously considered Givetian; *Stringocephalus burtini* had been reported from them but this record was doubted by Khodalevich *et al.* (1959). Also some of the sequences considered Lower Devonian or older by Soshkina are considered Eifelian by Spasskiy (1960a).

The correlation of the eastern sections one with another and of the western sections one with another and of the eastern with the western (including the type localities of Soshkina's species *Zelophyllia tabulata*, *Tryplasma magnum*, *Astrophyllum irgizlense*, *Neomphyma striata*, and *Fasciphyllum petschorense*), is still under discussion, the main

point at issue being how much of the sequence on either side should be regarded as lower and how much upper 'Eifelian'. Spasskiy (1955, 1959, 1960a, 1964) treated as lower Eifelian on the western slopes, the Takatin, Vanyashkin, and Vyazov beds and on the eastern slopes, the horizons D₂ 1 a-e of Andronov; he considered the Yaiva Band, the *Calceola* Beds, and the Biya beds of the western slopes as Upper Eifelian as also the Bogoslovsky bauxite horizon and overlying conchiferous limestone of the eastern slopes. Yanet (*in* Khodalevich *et al.* 1959) zoned the Eifelian of the eastern slopes into a lower zone of *F. regularissimus* and an upper *Conchidiella* zone; but this division does not necessarily coincide with Spasskiy's.

Khodalevich *et al.* (1959) considered the *F. regularissimus* zone to correlate with the Salairkin beds of the Kuznetsk sequences and the *Conchidiella* zone with the Shandin beds of that sequence.

Using Spasskiy's early and late Eifelian for the Rugosa, and for the Tabulata of the western slopes, and Dubatolov's (1964) division (following Yanet *in* Khodalevich 1959) for the eastern slopes, it is possible to distinguish an early Couvinian from a late Couvinian fauna. Both are clearly distinct from the 'Coblenzian' fauna and both contain many species in common, but there are a few generic and more specific differences. Taking the Rugosa first:

Continuing into the early Middle Devonian (*sensu* Spasskiy) from the 'Coblenzian' are *Pseudamplexus*, *Chlamydoephyllum tabulatum* (Soshk.), *Favistella*, *Dendrostella*, *Loyolophyllum*, *Fasciphyllum*, *Acanthophyllum*, *Neomphyma striata* Soshk., *Lyrielasma petschorense* (Soshk.), *Xystriphyllum*, *Spongophyllum halysitoides* Eth., *Tryplasma* and *Plasmophyllum* (*Plasmophyllum*). Newly appearing in the early Middle Devonian (*sensu* Spasskiy) are *Pseudopetraia*, *Barrandeophyllum*, *Nalivkinella*, *Keriophylloides astreiformis* (Soshk.), *Peneckiella porfirievi* Spasskiy, *Trapezophyllum brevisseptatum* (Yoh), '*Megaphyllum*' *juresanense* (Soshk.), '*Charactophyllum*' *antiquum* Soshkina, *Neocolumnaria*, *Stringophyllum*, *Plasmophyllum* (*Mesophyllum*), and *Calceola* (with thickened tabellae). This represents a very considerable enrichment of the late Lower Devonian fauna from which *Rhizophyllum* has nearly everywhere disappeared. In the late Eifelian occur the following genera not listed earlier from the Urals: *Cyathophyllum* (*Peripedium*) *spinulosum* (Soshk.), *Thamnophyllum*, *Plasmophyllum* (*Plasmophyllum*) [as *Pseudozonophyllum*, *Pseudomicroplasma*, and *Lythophyllum*], *P.* (*Mesophyllum*) [as *Arcoephyllum*, *Uralophyllum*, and *Glossophyllum*], '*Campophyllum*' *soetenicum* Schlüter and *Calceola* (without tabellae). A large number of species is common to both lower and upper parts of the Eifelian; however, *Pseudamplexus* is not reported from the Upper Eifelian of the Urals. From the undifferentiated Eifelian of the eastern slopes, Vaganova (*in* Khodalevich *et al.* 1959) figured solitary disphyllids (as *Tabulophyllum* and *Tortophyllum*), the phaceloid disphyllids *Paradisiphyllum simplex* (Vaganova), *P. caespitosum* (Vag.), and the cerioid '*Hexagonaria*' *massiva* (Vag.). The Rugosa have been described by Bulvanker (1934), Soshkina (1936, 1937, 1941, 1949 a, b, 1951, 1952), Markov (1941), Spasskiy (1955, 1959), and Pavlova (1965). Earlier papers on Devonian corals from the Urals are by Bogatyrev (1899), Chernyshev (1885, 1887, 1893), and Lebedev (1902).

The tabulatan fauna described by Yanet *in* Khodalevich (1959) from the Lower Eifelian *Favosites regularissimus* zone of the eastern slopes comprised *Favosites*, *Pachyfavosites*, *Squameofavosites*, *Thamnopora*, *Cladopora*, *Alveolites*, *Caliapora*, *Heliolites*, and *Syringopora*. Their stratigraphic significance was discussed by Yanet (1960). Tabulata

described by Sokolov (1952*b*) from the Vyazov beds of the western slopes are species of *Pachyfavosites*, *Crassialveolites*, and *Caliapora*. For the *Calceola* and Biya beds of the western slopes Sokolov has described (1952*b*) or recorded (1962*d*) species of *Favosites* including *F. goldfussi*, *Pachyfavosites*, *Emmonsia*, *Oculipora*, *Thamuopora*, *Striatopora*, *Cladopora*, *Corolites*, *Alveolites*, *Crassialveolites*, *Caliapora*, *Coenites*, *Natalophyllum*, and *Syringopora* (usually large). Yanet described from the Upper Eifelian *Conchidiella* zone of the eastern slopes species of the genera *Chaetetes*, *Favosites*, *Pachyfavosites*, *Emmonsia*, *Thamuopora*, *Cladopora*, *Alveolites*, *Alveolitella*, *Crassialveolites*, *Caliapora*, *Heliolites*, and *Syringopora*.

Russian Platform

Ermakova (1960, 1964, 1965) described from bore-cores from the south-eastern part of the platform species of several of the rugosan and tabulatan genera listed for the *Calceola* and Biya beds above and in addition the new phacelo-ceriod rugosan genus *Breviseptophyllum*.

Armenia

Soshkina (1952) figured *Macgeea nurchisoni* (Penecke), *Cyathophyllum* (*Peripaedium*) *spinulosum* (Soshk.), *Fasciphyllum orientale* Soshk., *Acanthophyllum* (as *Pseudochonophyllum*), *Plasuophyllum* (as *Lythophyllum*) from Armenian beds that she referred to the Eifelian. Ulitina (1963) has described *Plasmophyllum* species (as *Nardophyllum*) from the Rivers Arpa and Araks. In his Eifelian list Spasskiy (1964) included *Peneckiella bashkirica* (Spasskiy). Chudinova is working on the Tabulata of the Eifelian Volchevorot beds, including *Favosites goldfussi*, *Thamuopora*, *Alveolitella*, and *Heliolites*. Frech (*in* Frech and Arthaber 1900) described other corals some of which may have been Eifelian.

Central Asia

From the Eifelian mainly reef limestones of this region in Fergana, Tadzhikistan, the Pamir, and Darwas, Spasskiy (1964) listed †*Liudstroemia*, *Pseudopetraia*, *Barrandeophyllum*, **Oligophyllum*, **Tabulophyllum rotundum* Spasskiy, **Calceola*, †*Pseudamplexus*, *Chlaunophyllum* [as *Zelophyllia*] **Zmeinogorskia sagsaika* Spasskiy, *Tryplasma devonianum*, *Plasmophyllum* (*Plasmophyllum*), *Acanthophyllum*, **Campophyllum soetenicum* Schluter, **Heliophyllum halli*, **Favistella symbiotica*, **F. vulgaris* (Soshk.), *Spougophyllum halysitoides*, **Xystriphyllum altum* (Soshk.), *X. devonicum* (Bulv.), *Grypophyllum striatum* (Soshk.), †*Loyolophyllum*, cerioid and phaceloid *Fasciphyllum*, and *Neocolumaria*. Of these the ones marked * are from the upper parts only and those marked † from the lower parts only. Dubatolov (1964) listed from the Eifelian tabulatan fauna, which like the rugosan fauna is largely undescribed, *Favosites*, †*Pachyfavosites*, *Oculipora*, †*Squameofavosites*, **Caliapora* and *Heliolites*.

Goryanov (1963), working in S. Fergana, distinguished three rugosan assemblage zones; from the first two, the *Acanthophyllum*–*Ptenophyllum* zone and the *Columaria*–*Fasciphyllum* zone of the lower and middle parts of the Katran suite and which he regarded as correlative with the Takatin Vanyashkan and Vyazov beds of the Urals and the Salairkin beds of the margin of the Kuzbas, he listed but has not figured *Chlaunophyllum tabulatum* (Soshk.), *Petraia*, *Syringaxon*, *Barrandeophyllum*, *Heliophyllum*

spongiosum Schlüter, 'H'. cf. *antiquum* (Soshk.), *Loyolophyllum cresswelli*, *Neocolumnaria vagranensis* (Soshk.), *Acanthophyllum*, *Neomphymia striata* (Soshk.), *Fasciphyllum halliaforme*, *F. orientale*, and *F. conglomeratum* Schlüter, *Xystriphyllum* spp. (as *Stenophyllum*), and no *Plasmophyllum*.

From the *Stenophyllum*–*Zonophyllum* zone which he correlated with the *Calceola* and Biya beds of the western Urals, and the Shandin beds of the Salair, he listed *Nalivkinella*, *Barrandeophyllum*, *Mucophyllum biseptatum* (Soshk.), *Grypophyllum*, *Xystriphyllum*, *Fasciphyllum*, *Columnaria*, 'Campophyllum' *soetenicum*, 'Heliophyllum spongiosum' (Schlüter), 'H' *antiquum* (Soshk.) and *Plasmophyllum* (*Plasmophyllum*) [as *Zonophyllum*], and *P. (Mesophyllum)* [as *Digonophyllum*].

Kazakhstan

Spasskiy (1965) described from rocks considered Eifelian in the Dzhungarian Alatau, the new genus *Multicarinothyllum*, 'Bethanythyllum' *maximum* Spasskiy, and *Spongothyllum gemmatum* Spasskiy and listed *Barrandeophyllum*, *Orthopaterophyllum*, *Ridderia*, *Acanthophyllum*, *Stringophyllum* and *Plasmophyllum* (*Mesophyllum*) [as *Digonophyllum*], and *Favosites*, *Thamnopora*, and *Tyrganolites*. His 1964 list included *Eddastrea grandis* (Dun) (= *Tainiropyllum*). From the northern sub-Balkash Dubatolov (1964) listed the undescribed late Eifelian tabulatan fauna as species of *Squameofavosites*, *Thamnopora*, *Cladopora*, *Coenites*, *Placocoenites*, *Tyrganolites*, *Stelliporella*, and *Syringopora* and Spasskiy (1964) listed *Thamnothyllum*, *Campophyllum maximum* Spasskiy, *Heliophyllum halli* E. & H., and *Cyathophyllum* (*Peripaedium*) *spinulosum* (Soshk.). I have seen no figures of this interesting fauna, which presumably is late Eifelian. Sharkova (1963b) has described the middle Devonian Tabulata of the Tarbagatay Range.

Altai–Sayan Geosynclinal Region

The Salairkin beds with *Paraspirifer gurievskensis* were considered Zlichovian by Rzhonsnitskaya (1962) and Upper Emsian; but she included these correlatives in the Middle Devonian with the Assise de Bure of the Ardenne, which she regarded as older than the Eifelian. Dubatolov (1964) lists the Salairkin beds as early Eifelian.

Rugosa of the standard sections have been described by Peetz (1901), Bulvanker (1958), Kraevskaya (1955b), and Zheltonogova and Ivaniya (1961) and comprise *Thamnothyllum*, *Disphyllum*, *Loyolophyllum*, *Acanthophyllum*, *Xystriphyllum massivum* (Bulv.), *X. submassivum* (Bulv., with columella), *X. devonicum* (Bulv.) and *X. gorskii* (Bulv.), 'Grypophyllum' *gracile* (Soshk.), *Spongophyllum* [or? *Australophyllum*], *Plasmophyllum* (*Plasmophyllum*) (as *Pseudomicroplasma*). The species referred to *Iowaphyllum* in Zheltonogova and Ivaniya (1961) seems rather to be *Endophyllum*—possibly the earliest of that genus. See also Ivaniya (1965).

Spasskiy (1960 c, d) described some Rugosa from the southern Altai and neighbouring regions, including a small fauna from the lower part of the Lower Kultabar suite which may be Lower Devonian, but possibly is as young as the Salairkin faunas of the Salair.

Tabulata from the Salairkin beds have been described by Peetz (1901), Chernyshev (1951), Chudinova (1959, 1964), Dubatolov (1956a, b, c, 1959, 1962, 1963, 1964), Dubatolov and Mironova (1961a, b, c), Dubatolov and Chekhovich (1964), and Dubatolov and Smirnova (1964). They comprise *Favosites regularissimus* Yanet and other species of *Favosites*, rare *Squameofavosites*, *Pachyfavosites polymorphus* (Goldfuss),

Gephuropora, *Striatopora*, *Gracilopora*, *Thamnopora*, *Cladopora*, *Placocoenites*, *Egosiella*, *Lecomptia*, *Alveolites*, *Coenites*, *Caliapora*, *Grabaulites*, *Armalites*, *Syringopora*, *Roemeripora* (also named as *Loyolophyllum brevisseptatum* Bulv.), and *Roemerolites*. Many of the favositid species are unknown earlier. Khalfin (1961) considered it possible that the lower part of the Salairkin beds may represent the upper Emsian.

The Shandin beds of the South-west Kuz basin and North Salair standard sections are generally accepted as Eifelian, and most Russian authors consider them equivalent to part of the Upper Couvinian (Co₂). The Rugosa of the standard Salair sections have been described by Peetz (1901), Chernyshev (1930), Bulvanker (1958, 1963), Ivaniya (1957a, 1958b, 1960, 1961), Zheltonogova and Ivaniya (1961), and those of neighbouring regions by Spasskiy (1960c, d), Bulvanker in Rzhonsnitskaya *et al.* (1952), Bulvanker in Rzhonsnitskaya and Meleschenko (1955). They comprise species of *Barrandeophyllum*, *Thamnophyllum*, *Eridophyllum* [?] *asiaticum* Ivan., *Dendrostella*, *Loyolophyllum*, *Sinospongophyllum major* (Bulv.), *Acanthophyllum*, *Xystriphyllum* spp. [as *Stenophyllum*], fasciculate *Fasciphyllum halliaforme* Soshk., *Taimyrophyllum carinatum* Bulv. [?= *Aphroidophyllum* Lenz, 1961], *Calceola*, *Plasmophyllum* (*Plasmophyllum*) and *P.* (*Mesophyllum*). Lists are given by Spasskiy (1964). See Ivaniya (1965).

The Tabulata of the standard South-west Kuz Basin margin and Salair sections of the Shandin beds have been described by Chernyshev (1951), Dubatolov (1959, 1963, 1964), Chudinova (1959, 1964) and Dubatolov and Mironova (1961a, b, c) and comprise *Favosites goldfussi* d'Orb., *Pachyfavosites polymorphus* (Goldfuss), and species of *Squameofavosites*, *Enimonsia*, *Fomitchevia*, *Pleurodictyum*, *Striatopora*, *Thamnopora*, *Cladopora*, *Alveolites*, *Crassialveolites*, *Caliapora*, *Placocoenites*, *Egosiella*, *Tyrganolites*, *Armalites*, *Natalophyllum*, *Syringopora*, *Heliolites*, *Pachycanalicula*, *Chaetetes*, and *Cyclochaetetes*.

In addition, Kraevskaya (1955b) described from the undivided Eifelian (i.e. Salairkin plus Shandin beds), *Pseudospongophyllum massivum* Kraevskaya [? = *Xystriphyllum*], and '*Pseudochonophyllum*'.

Eifelian Tabulata of neighbouring regions have been described from the Mountainous, Southern, and Rudny Altai by Dubatolov and Mironova (1961a, b, c), Dubatolov (1952, 1953, 1955, 1962), and Chudinova (1955, 1959) and from Mongolia and Tuva by Chernyshev (1937b). Chudinova (1965) has discussed their palaeoecology. *Tyrganolites* and *Thecostegites* are included in the descriptions from the Losishin beds of the Rudny Altai and *Adetopora* is found in the Tashtyp beds of the Minussinsk trough. Eifelian Rugosa of neighbouring regions have been described from the Mountainous, Southern, Rudny, and Mongolian Altai by Spasskiy (1960c, d, 1965), Bulvanker *et al.* (1960), Besprozvannykh (1964), Bulvanker in Rzhonsnitskaya *et al.* (1952), and Bulvanker in Rzhonsnitskaya and Meleshchenko (1955). The faunas are in general similar to those of the Shandin or Mamontov beds or both, but *Minusiella* occurs in the Tashtyp Formation of the Minussinsk trough (considered equivalent to the Shandin beds); *Sinospongophyllum* (as *Tabulophyllum rotundum*) and *Taimyrophyllum* occur in the Losishin beds, *Ridderia* in the Kryukov and Sokolin beds, *Australophyllum* (as *Spongophyllum kurgaense*) in the Rakitin beds, all three formations being regarded as Lower Eifelian. *Stringophyllum* is recorded by Besprozvannykh (1964) from the Eifelian Ust'-Kamen beds. *Rhizophyllum mongolicum* Spasskiy with '*Heliophyllum*' *antiquum* (Soshk.) occurs in the Mountainous Altai in beds considered equivalent in age to the Shandin

beds and *Zmeinogorskia* makes an early appearance at the same horizon but not in the same locality (Spasskiy, 1960c).

The Mamontov beds of the standard South-west Kuz-North Salair sections have been regarded as late Eifelian by Dubatolov (1959) and Rzhonsnitskaya (1962) but as Givetian by Chudinova (1964). Rzhonsnitskaya lists the upper Eifelian *Pinacites jugleri* as of the Mamontov fauna but its locality is unknown to me; in the overlying Akarchatkinsk horizon she lists *Maeneceras* regarded as Givetian. Spasskiy (1962) has discussed the boundary between the Eifelian and Givetian stages in the light of the rugosan faunas.

The Rugosa of the Mamontov beds described by Ivaniya (1957, 1958), Zheltonogova and Ivaniya (1961), and Bulvanker (1958) are *Dendrostella*, *Fasciphyllum* [?] *kuznet-skiense* Ivaniya, *Grypophyllum gracile* (Wdkd.), *Xystriphyllum* spp., *Stringophyllum* (*Sociophyllum*) sp., *Plasmophyllum* (*Plasmophyllum*). See also Ivaniya (1965).

The Tabulata of the Mamontov beds are *Favosites*, *Squameofavosites*, *Pachyfavosites*, *Thamnopora*, *Cladopora*, *Alveolites*, *Alveolitella*, *Crassialveolites*, *Placocoenites*, *Tyrganolites*, *Heliolites*, *Thecostegites*, and *Chaetetes* (Chernyshev 1951; Dubatolov 1959, 1963; Dubatolov and Mironova 1961a; and Chudinova 1959, 1964). Dubatolov considered that *Squameofavosites*, not known elsewhere above Eifelian equivalents, indicates that the Mamontov beds are Eifelian.

Taimyr

From the Middle Devonian of the Taimyr Spasskiy (1964) listed **Campophyllum soeticum* Schlüter, **Favistella quadrisepata* Soshk., *Acanthophyllum*, *Neophyma striata* (Soshk.), *Xystriphyllum* [as *Stenophyllum*], **Fasciphyllum* cf. *orientale* (Soshk.), **Diplochone*, *Plasmophyllum* [as *Pseudozonophyllum*], and **Plasmophyllum* (*Mesophyllum*) [as *Digonophyllum*]. Those marked * are considered late Eifelian. Dubatolov and Smirnova (1964) listed *Favosites regularissimus* Yanet, *Pachyfavosites*, *Squameofavosites*, *Pleurodictyum*?, *Alveolites*, *Crassialveolites*, and *Syringopora*. Smirnova (1965b) described new species.

North-eastern U.S.S.R.

Bulvanker (1965) figured from strata in the Ormulev regions referred to the Eifelian, '*Campophyllum*' *soeticum* Schlüter, *Anlacophyllum* [?] *Minussiella solida* Bulv. [= *Hexagonaria quadrigemina* group], *Grypophyllum*, *Plasmophyllum versiforme* (Markov), and *P. latum* (Soshk.); Spasskiy (1964) added *Taimyrophyllum* and *Pseudamplexus altaicus* to the list.

The Eifelian Tabulata of the Tas-Khayakhtakh, Sette-Daban, and Ormulev Mt. regions (Dubatolov 1964) form a unit, though different families predominate in the Ormulev Mts. The genera are: *Favosites*, *Pachyfavosites*, *Squameofavosites*, *Thamnopora*, *Cladopora*, *Alveolites*, *Crassialveolites*, *Alveolitella*, *Caliapora*, *Coenites*, *Placocoenites*, *Heliolites*, and *Syringopora*.

Faunal Analysis and Palaeozoogeography

The early Couvinian fauna (of the Salairkin beds and their equivalents) is less sharply distinguished from that of the late Lower Devonian than the latter was from the Tiverian; its most important rugosan genera are *Barrandeophyllum*, *Pseudamplexus*, *Chlamydo-phyllum*, *Loyolophyllum*, *Favistella*, *Acanthophyllum*, *Neophyma*, *Fasciphyllum*,

Xystriphyllum, and *Spougophyllum*, all these being known in the late Lower Devonian. But rare *Neocolumnaria*, *Keriophylloides*, *Trapezophyllum*, '*Charactophyllum*' *antiquum*, *Stringophyllum*, and *Calceola* appear. The tabulatan fauna is characterized by the rapid development and dominance of thick-walled *Thamnopora* and *Cladopora* which begin to displace the favositids, by the wide distribution of thick-walled favositids (*Pachyfavosites*, *Oculipora*, *Gephuropora*) that were still sparse earlier (Yanet 1965), by the reduction in importance of *Squameofavosites* and *Favosites*, by the wider distribution of thick-walled alveolitids, and by the occurrence in many regions of *Favosites regularissimus*.

Zoogeographical provinces of the early Couvinian are the same as those of the later Lower Devonian, but the Uralo-Tien Shan province shows great uniformity and the Altai-Sayan province is rather distinct, differing in the large number of *Xystriphyllum* spp. and the absence of *Pseudamplexus*.

The late Couvinian faunas (Shandin and Mamontov) began to luxuriate with wide transgressions of the sea, and in Asia both Rugosa and Tabulata reached their Devonian acme with a remarkable number of genera, species, and individuals. The most characteristic rugosan genera are *Ridderia*, *Oligophyllum*, '*Campophyllum*' *soeticum*, *Heliophyllum* including '*H.* *antiquum*' (Soshkina), *Cyathophyllum* (*Peripaedium*), *Thamnophyllum*, *Macgeea*, *Neocolumnaria*, *Favistella*, '*Grypophyllum*', *Fasciphyllum*, *Xystriphyllum*, '*Tabulophyllum*', *Plasmophyllum* (*Plasmophyllum*) [as *Pseudomicroplasma*, *Lythophyllum*, *Nardophyllum*, *Zonophyllum*, *Pseudozonophyllum*], and *Plasmophyllum* (*Mesophyllum*) [as *Arcophyllum*, *Digonophyllum*], and *Calceola*.

Of the Tabulata, thamnoporids, alveolitids, and coenitids showed remarkable development; *Thamnopora* and *Cladopora* dominate and with them may occur *Striatopora* and *Fomitchevia*; strong development of wall thickening, of septal elements, and of mural pores characterize the first two. Alveolitids continued to develop thickening of their skeletal elements. *Caliapora* and *Coenites* reached their acme and the appearance of *Placocoenites*, *Tyrganolites*, and *Natalophyllum* is typical for this time. The favositids have waned, *Pachyfavosites* is less numerous, *Squameofavosites*, *Gephuropora*, and *Plicatomurus* have become extinct before the Givetian.

The earlier zoogeographic provinces became less distinct; by the late Couvinian the Uralo-Tien Shan and the Altai-Sayan provinces had become one, to which also the Caucasus and Western Europe belonged, or at least were in communication. The Mongolo-Okhotsk and Indigiro-Kolyma provinces and the Taimyr region also showed immense similarity to the Altai-Sayan region of this common province, with easier diffusion of species. Nevertheless, there were still some provincial differences, such as the occurrence of *Minussiella* in the Minussinsk-Tuva region.

Within the limits of the U.S.S.R. the Givetian faunas are found in smaller areas than the late Eifelian fauna, and are less rich in genera and species.

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MARIOPTERIS FROM THE STEPHANIAN OF NORTH-WEST SPAIN

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ABSTRACT. Three species of *Mariopteris* are described from Stephanian B-C rocks in North-west Spain. The record is based only on five specimens, but it proves that *Mariopteris* was by no means extinct by Lower Stephanian times, as so often has been stated in the literature. The validity of the genus *Pseudomariopteris* is questioned.

WHEN collecting in the Tineo coalfield of Asturias, North-west Spain, one of the present writers (C. A.-R.) discovered and identified a few specimens of well-preserved *Mariopteris* among numerous remains of a well-characterized assemblage of Stephanian B-C flora, probably representing lower Stephanian C (compare Zeiller 1882; Meléndez 1943; Menéndez Amor and Jongmans 1952, 1954; Alvarez-Ramis 1964; Doubinger and Alvarez-Ramis 1963, 1964; de la Vega Rollán 1964; Wagner 1964, 1966). The occurrence of *Mariopteris* in such a Late Carboniferous assemblage seemed most unusual, since it has been repeatedly stated in the literature that Stephanian floras are characterized by the absence of *Mariopteris*, which would be restricted to Namurian and Westphalian strata (Jongmans and Pruvost 1950, p. 343; Gothan and Weyland 1954, p. 438). Such a negative characteristic is obviously unreliable and it has been known for a long time (Huth 1912) that the range of *Mariopteris* extended into Lower Stephanian. However, the record of *Mariopteris zeilleri* Huth is based on a single specimen only, so that it might still be regarded as generally true that *Mariopteris* would not be an element of Stephanian floras. Also records provided by one of the present authors (Wagner in Kanis 1956; and Wagner 1964, 1966), relating to the presence of *Mariopteris nervosa* (Brongniart) and *Mariopteris* sp. (cf. *rotundata* Huth) in basal Stephanian rocks of North-west Spain (viz. strata assigned to the newly proposed 'Cantabrian' Stage), do not materially alter the general statement of an absence of *Mariopteris* in the Stephanian proper (i.e. in strata of equivalent age to that of the Stephanian in Central France). An obviously different case is presented by the specimens described in the present paper. Not only have these specimens been found in rocks of fairly late Stephanian age, but they also show considerable diversification. Although the actual number of specimens collected is very small (only four specimens having been recovered from the Tineo coalfield), they are judged to belong to two different species. One more specimen, representing an additional species, has been determined from a collection made by Dr. W. F. M. Kimpe from upper Stephanian B rocks in the eastern part of the Villablino coalfield (province of León). A list of fossils dating this locality is given on p. 702 of the present paper. Only one of the specimens found in Stephanian B-C strata of North-west Spain has been completely identified with a known species of Westphalian age. The other specimens are considered to belong to new species. However, they show a close similarity with some Westphalian species recorded in the literature.

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numerous other plant remains collected in the course of his investigations on the coalfield of Villablino (León). They are also grateful for facilities in the Department of Geology, University of Sheffield, where Mr. B. Pigott took the photographs illustrating this paper.

DESCRIPTION OF SPECIES

Mariopteris cantabrica sp. nov.

Pl. 104, figs. 1, 2; Pl. 105, fig. 1; text-fig. 1

1964 *Mariopteris* cf. *latifolia* Alvarez-Ramis (*non* Brongniart), p. 73, lám. III, fig. 4.

Material. Only one reasonably well-preserved specimen (holotype) and a more fragmentary remnant of this plant are available for description. The holotype is a negative.

Description. Pinnae of the penultimate order with alternate side pinnae inserted at wide angles, varying probably from 70° to 80° (60–90° on the holotype, due to tectonic deformation). Rachides of the penultimate order winged and somewhat grooved longitudinally; 3–4 mm. wide. Pinnae of the last order closely spaced and even partly overlapping; both catadromous and anadromous basal pinnules clearly bilobate in pinnae of average position in the frond. Rachides of the last order rounded, with irregular small costae; rachides up to 1 mm. wide. Pinnules inserted at 60–70° angles; adhering to the rachis with almost the entire basal width in the upper parts of pinnae, and generally becoming more sphenopteroid in the lower parts, though always retaining a relatively broad insertion (never inserted by the midvein only). Pinnules in the upper parts of pinnae probably entire (conjectural because of the fragmentary condition of the holotype), for those in the middle parts possess only slightly undulate margins. Lower pinnules clearly lobed, and basal pinnules clearly bilobate. Pinnules approximately 2½–3 times as long as broad. Lobes rounded, relatively wide, generally about twice as long as broad, and rather steeply inclined to the midvein (approximately 60°). Pinnule lamina apparently rather thin, though not so thin as to appear flat on the rock surface. Midvein decurrent, generally straight, sometimes slightly flexuous. Nervules steeply inclined (approximately 30° to the midvein), repeatedly bifurcate, thin and fairly numerous (approximately 35 veins per cm. on the pinnule border). Fructifications unknown.

Type. Holotype figured on Pl. 104, figs. 1, 2 (and Pl. 105, fig. 1). Origin: tip of the seam Purita, lower Stephanian C, Tineo coalfield (Asturias, North-west Spain). Repository of holotype and unfigured specimen: Instituto 'Lucas Mallada', Consejo Superior de Investigaciones Científicas, Paseo de la Castellana 84, Madrid (coll. Alvarez-Ramis).

Derivatio nominis. The Cordillera Cantábrica in North-west Spain.

Diagnosis. Winged rachides with closely spaced, partly overlapping pinnae; both catadromous and anadromous basal pinnules clearly bilobate. Ordinary pinnules entire to lobate, with rounded, rather steeply inclined lobes; insertion fairly broad; lamina thin. Midvein decurrent; nervules thin, steeply inclined, fairly numerous.

Comparison. The Westphalian species *Mariopteris guthoerli* Lutz is closely similar in the shape and dimensions as well as the insertion of the pinnules which are also rounded lobed to entire as in *Mariopteris cantabrica* sp. nov. However, the two species differ in

the apparently somewhat thicker lamina of *M. guthoerli* which may also possess rather less steeply inclined nervules. Lutz (1938) observed that the rachides of *M. guthoerli* possessed faintly marked transverse bars, additional to more clearly expressed longitudinal grooves. Such transverse bars have not been found on the rachides of *M. cantabrica*.



TEXT-FIG. 1. Nervation diagram of some pinnules from the holotype of *Mariopteris cantabrica* sp. nov. as figured on Pl. 104, fig. 1 and Pl. 105, fig. 1 (based on a photographic enlargement, $\times 6$). These lobed pinnules occupy a relatively low position in the pinna.

Mariopteris witieri Corsin is also characterized by little lobed, broadly based pinnules, but there the resemblance ends, for this species is further characterized by rachides with strongly marked transverse bars and massive looking, confluent pinnules with a thick lamina. Its basal pinnules are not very strongly bilobate.

Mariopteris sauveuri (Brongniart) Stur has more widely spaced pinnae with relatively broader and more sturdy looking pinnules than those occurring in *Mariopteris*

EXPLANATION OF PLATE 104

- Figs. 1, 2. *Mariopteris cantabrica* sp. nov.; from tip of the seam Purita, lower Stephanian C, Tineo coalfield in Asturias, North-west Spain. 1, Holotype, $\times 1$, showing bilobate catadromous and anadromous pinnules; and well-developed ordinary pinnules in probably the lower middle part of pinnae of the penultimate order. 2, Enlargement ($\times 3$) of some lobing pinnules in lower part of specimen.
- Fig. 3. *Mariopteris melendezi* sp. nov.; from tip of the seam Purita, lower Stephanian C, Tineo coalfield in Asturias, North-west Spain. Holotype, $\times 1$, showing fragments of pinnae with fairly small pinnules characterized by a semi-perpendicular insertion and rounded lobes.
- Figs. 4, 5. *Mariopteris colliciaris* D. White; from tip of seam 6, Carrasconte coal group, upper Stephanian B, Villablino coalfield, province of León, North-west Spain. 4, Specimen ($\times 1$) showing typically sphenopteroid pinnules with convex, rounded lobes; on the same slab are *Pecopteris jongmausi* Wagner and *Sphenophyllum oblongifolium* Germar and Kaulfuss. 5, Enlargement ($\times 3$) of main part of pinna fragment on left side of specimen.



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cantabrica sp. nov. The former species also appears to be characterized by a rather thick pinnule lamina. Its pinnules are even more generally entire than those of *M. cantabrica*.

Mariopteris muricata (von Schlotheim) *sensu* Zeiller has generally smaller, more rigid pinnules which are also narrower than those of *Mariopteris cantabrica* sp. nov. They also appear to be generally more entire than those of the latter. The pinnae of *M. muricata* may be less closely spaced than those of *M. cantabrica*.

Remarks. The holotype of *Mariopteris cantabrica* (Pl. 104, fig. 1) shows fragments of pinnae which probably belong to the lower middle parts of pinnae of the penultimate order. Only the lower parts of side pinnae (of the last order) are preserved, but it appears evident that a rather large proportion of the pinnules in the frond were either entire or nearly entire. Lobed pinnules show rather short, rounded lobes of a similar shape to those visible on the type specimen of *Mariopteris guthoerli* Lutz (see Lutz 1938, Taf. XIX, figs. 4, 4A). On the whole, Lutz's specimen possesses more entire pinnules, but this feature may well be ascribed to a slightly higher position within a pinna of the penultimate order than that occupied by the holotype of *Mariopteris cantabrica* sp. nov. This impression is strengthened by the fact that the unlobed pinnules of the latter show exactly the same proportions (i.e. approximately 10×4 mm.) as those of the former, whereas the lobed pinnules of *M. cantabrica* are larger and relatively longer (as can be expected for lobing segments). It would therefore be quite possible to identify *M. cantabrica* with *M. guthoerli*, if it did not appear that *M. cantabrica* possessed a relatively thinner pinnule lamina as well as apparently more widely spaced nervules than *M. guthoerli*. Moreover, Lutz recorded that *M. guthoerli* possessed faint transverse bars on the rachides. Although this feature is hardly visible on the illustration of the holotype of this species (Lutz 1938, Taf. XIX, figs. 4, 4A), it should be an important characteristic, since Danzé-Corsin (1953, p. 53) decided that the subdivision of *Mariopteris* could be to a large extent based on this characteristic. She noted that most of the species of *Mariopteris* were characterized by the presence of transverse bars on the rachides (i.e. the group *Lineae*), whilst only a few species showed only longitudinal striae or grooves on the rachides and climbing stem (group *Alineae*). *M. cantabrica* apparently belongs to the *Alineae* and therefore has to be considered as quite different from *M. guthoerli* (of the *Lineae*), even though the pinnules of both species are rather similar. It may, however, be noted as well that the basal pinnules of *M. cantabrica* are more strongly bilobate than those of *M. guthoerli*, thus adding another means of differentiation.

There is an appreciable difference in stratigraphic age between these two species, for *Mariopteris guthoerli* Lutz has been recorded from the Westphalian C (Saar-Lorraine area), whilst *Mariopteris cantabrica* sp. nov. has been found in lower Stephanian C rocks. Both species are known from single specimens only, however.

As far as known to the present authors, there is only one record in the literature which may point to a wider range for *M. cantabrica*. It deals with a rather fragmentary specimen from upper Westphalian D rocks in northern Portugal, which has been figured under the name of *Mariopteris* cf. *muricata* (von Schlotheim) by Teixeira (1942, Est. IV, figs. 2-3). Unfortunately, this specimen, which shows a marked resemblance to *Mariopteris cantabrica*, appears too fragmentary to be identified with certainty.

Occurrence. Lower Stephanian C, tip of the seam Purita, Tineo coalfield, Asturias, North-west Spain.

Mariopteris melendezi sp. nov.

Plate 104, fig. 3; Plate 105, fig. 2; text-fig. 2

1964 *Mariopteris* sp. Alvarez-Ramis, p. 73, lám. III, fig. 5.

Material. The description is based on two specimens, one of which is a negative (holotype). The second specimen is too fragmentary to be figured.

Description. Rachis of the penultimate order slightly winged, irregularly grooved in longitudinal direction, relatively wide (2 mm.). Pinnae of the last order inserted at angles of approximately 60°; alternating, closely spaced, and partly somewhat overlapping; apparently rather quickly tapering in the apical portions. Rachides of the last order fairly thin (0.5 mm. wide) and irregularly grooved in longitudinal direction. Pinnules small, completely adherent to the rachis, and even decurrent on the basiscopic side; inserted slightly obliquely though nearly perpendicular in the lower parts of pinnae; approximately 2½ times longer than they are broad. Pinnules always lobate, with shallow sinuses. Lobes rounded to somewhat denticulate. Basal catadromous pinnules bilobate. Pinnule lamina probably of average thickness. Midvein almost as thin as the nervules; generally non-decurrent, sometimes rather flexuous. Nervules widely spaced (approximately 10–12 veins per cm. on the pinnule border), repeatedly forked at fairly wide angles; generally not very steeply inclined. Fructifications unknown.

Type. Holotype figured on Plate 104, fig. 3 (and Pl. 105, fig. 2). Origin: tip of the seam Purita, lower Stephanian C, Tineo coalfield (Asturias, North-west Spain). Repository of type as well as unfigured second specimen: Instituto 'Lucas Mallada', Consejo Superior de Investigaciones Científicas, Paseo de la Castellana 84, Madrid (coll. Alvarez-Ramis).

Derivatio nominis. Professor B. Meléndez, University of Madrid, who has consistently furthered research on the Carboniferous of Spain.

Diagnosis. Pinnae probably rather short, and tapering rapidly in the apical part. Pinnules small, inserted at wide angles; adherent with the entire base, and decurrent on the basiscopic side; always lobate, with rounded to slightly denticulate lobes. Only basal catadromous pinnules are bilobate. Nervation wide, with thin, often flexuous midvein and repeatedly forking laterals.

Comparisons. *Mariopteris zeilleri* Huth appears to have more clearly winged and probably stronger rachides than those occurring in *Mariopteris melendezi* sp. nov. It also possesses bilobate basal pinnules on both the catadromous and the anadromous sides of pinnae, and shows rather strong midveins. *M. melendezi* has apparently only bilobate basal pinnules on the catadromous side, and possesses thin midveins. The shape

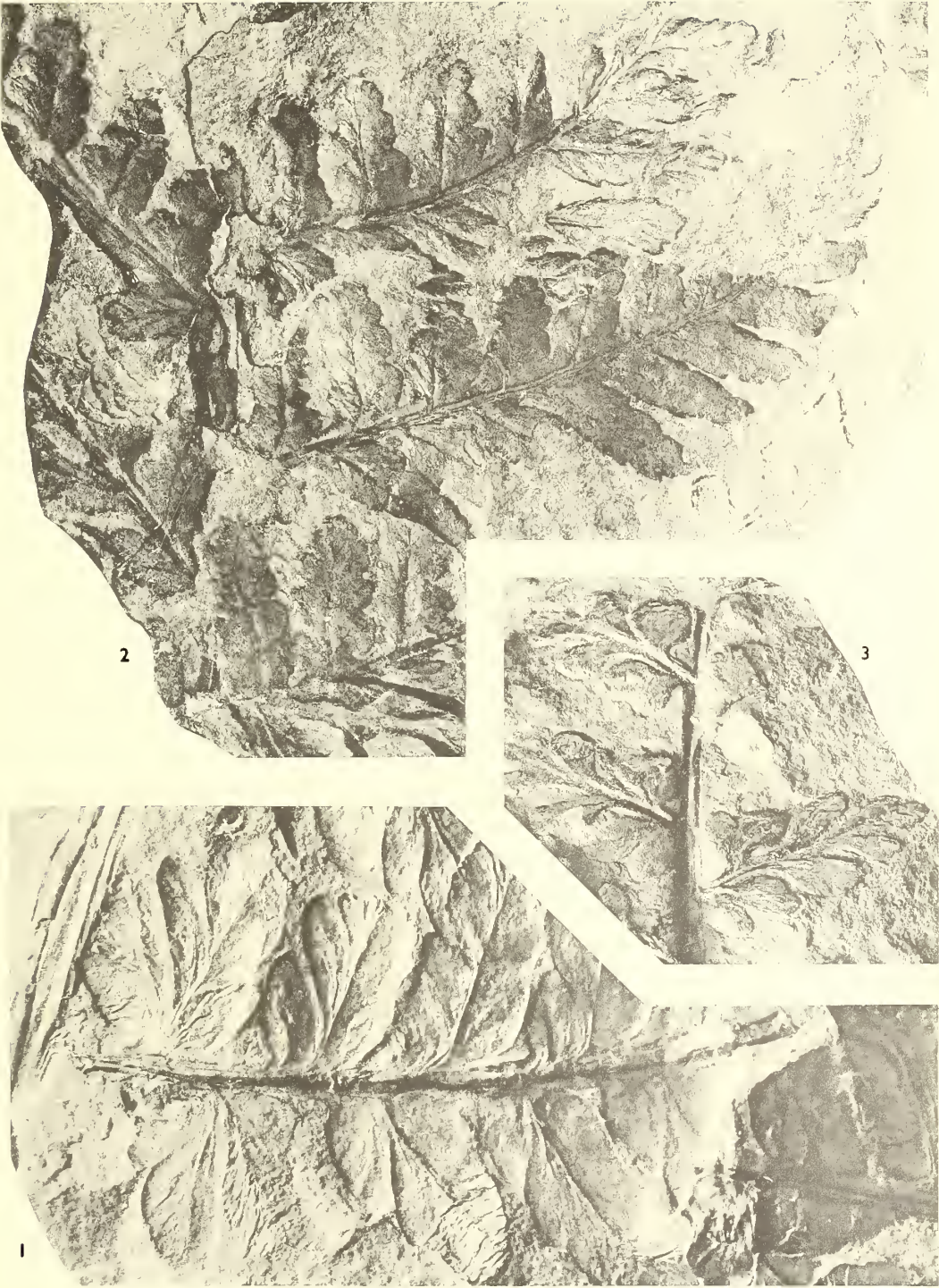
EXPLANATION OF PLATE 105

Fig. 1. *Mariopteris cantabrica* sp. nov. Enlargement (×3) of upper right part of holotype, showing bilobate basal pinnules.

Fig. 2. *Mariopteris melendezi* sp. nov. Enlargement (×3) of holotype showing fairly thin pinnule lamina and rounded lobes of pinnules.

Fig. 3. *Mariopteris colliciaris* D. White. Enlargement (×3) of lower right part of specimen figured on Plate 104, fig. 4, showing typically sphenopteroid pinnules with convex lobes.

Localities are given in the explanation of Plate 104.



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of the pinnules is fairly similar in both species, particularly with regard to the somewhat denticulate lobes (which are perhaps somewhat more strongly expressed in *M. zeilleri*).

Mariopteris guillaumei Corsin shows some similarity to *Mariopteris melendezi* sp. nov. in the general aspect and insertion of the pinnules which are also characterized by rounded lobes. However, its pinnules appear to be generally larger, somewhat more obliquely inserted and, on the whole, more entire than those of *M. melendezi*. It is also noted that the rachides of *M. guillaumei* possess strongly marked, closely set transverse bars.

Mariopteris daviesi Kidston possesses larger pinnules with more clearly pointed lobes, and thus differs markedly from *Mariopteris melendezi* sp. nov., even though in both species the pinnules tend towards a perpendicular insertion. The rachides of *M. daviesi* possess widely spaced transverse bars, a characteristic which has not been observed in *M. melendezi*.

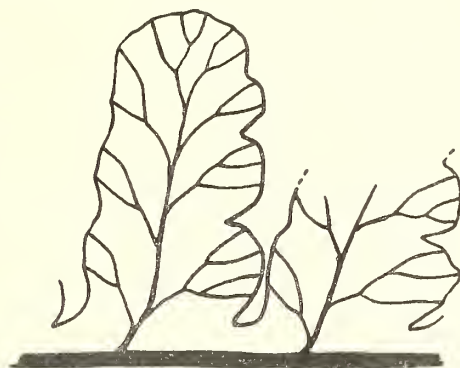
Mariopteris tenuis Bell shows a faint resemblance to *Mariopteris melendezi* sp. nov., but possesses larger pinnules with probably a somewhat thinner lamina than that occurring in the latter.

Mariopteris beneckeii Huth possesses somewhat larger, more obliquely inserted pinnules which are also more sphenopteroid than those of *Mariopteris melendezi* sp. nov. Both the catadromous and the anadromous basal pinnules of *M. beneckeii* are clearly bilobate.

A comparison with *Mariopteris hirsuta* Corsin shows the presence of more roundly lobed pinnules in *Mariopteris melendezi* sp. nov., as well as the absence of hairs on the underside of pinnules (which is a characteristic feature of *M. hirsuta*).

Remarks. The two specimens available for the description of *Mariopteris melendezi* sp. nov. are both fragments of the middle parts of pinnae; thus showing the average type of pinnules occurring in this species. One of the most striking characteristics found is the broad insertion of the pinnules which are even decurrent on the basiscopic side and which appear to be mainly confluent. This insertion is comparable to that of pinnules in the genus *Dicksonites* which also belongs to the Mariopteridaceae (see Corsin 1961; Danzé-Corsin 1953). A comparison with *Dicksonites* is strengthened by the tendency towards an almost perpendicular position of the pinnules in *M. melendezi*. On the other hand, the clearly bilobate basal pinnules, a characteristic which is unfortunately not very well brought out by the photograph on Plates 104, 105, definitely preclude an attribution to *Dicksonites*. The species discussed here also lacks the strong rachides which form one of the salient features of *Dicksonites*.

The occurrence of *Mariopteris cantabrica* sp. nov. and *Mariopteris melendezi* sp. nov. together in the same locality naturally invites speculation on the possibility that they might be conspecific. Both species belong to the same group of *Mariopteris*, viz. the *Alineae* Danzé-Corsin which are characterized by the absence of transverse bars on the



TEXT-FIG. 2. Nervation diagram of some pinnules from the holotype of *Mariopteris melendezi* sp. nov. as figured on Plate 104, fig. 3 and Plate 105, fig. 2 (based on a photographic enlargement, $\times 6$).

rachides. Furthermore, both species possess rounded lobes, although these tend to be slightly pointed in *M. melendezi*. There the comparison ends however. *M. cantabrica* has relatively larger, more obliquely inserted pinnules with more closely spaced nervules; the nervation being clearly wider in *M. melendezi*. Pinnules of equivalent size in *M. melendezi* are more lobate than those of *M. cantabrica*, which tend to be more entire. Moreover, the basal pinnules of *M. cantabrica* are more distinctly bilobate than those of *M. melendezi*.

Occurrence. Lower Stephanian C, tip of the seam Purita, Tineo coalfield, Asturias, North-west Spain.

Mariopteris colliciaris D. White

Plate 104, figs. 4, 5; Plate 105, fig. 3

- 1943 *Mariopteris paddocki* var. *colliciaris* D. White, p. 87, pl. 12, figs. 1–2, pl. 13, figs. 1–9.
cf. 1955 *Mariopteris sphenopteroides* Daber (*non* Lesquereux), p. 18, Taf. IV, fig. 3, Taf. XVI, figs. 1–3.

Material. Only a single specimen (positive) is available for description.

Description. Rachides of the penultimate order rather thin (up to 1 mm. wide), grooved and provided with somewhat indistinct transverse bars. Pinnae of the last order short and composed of 5–7 pinnules; pinnae inserted at approximately 50° angle to the rachis. Rachides of the last order thin. Pinnules inserted by part of the basal width only; decurrent on the basiscopic side and often tending towards insertion by the midvein only (sphenopteroid insertion); approximately as long as wide or only a little longer than wide, and rather small; entire or shallowly lobed, with rounded, somewhat oval lobes. Both the catadromous and the anadromous basal pinnules bilobate. Pinnule lamina apparently rather sturdy, since the pinnules are rather markedly convex (vaulted). Midvein little marked or virtually absent. Nervules thin, rather inconspicuous, and repeatedly forked.

Origin and repository of the figured specimen. Origin: tip of the seam 6 of the Carrasconte coal group, upper Stephanian B, Villablino coalfield (province of León, North-west Spain). Repository: Geologisch Bureau voor het Nederlandse Mijng gebied, Heerlen, Netherlands, Catalogue No. 47333 (coll. Kimpe, loc. 203).

Diagnosis. Thin rachides, longitudinally grooved with faint transverse markings; bearing short pinnae of the last order consisting of sphenopteroid, shallowly lobed pinnules with rounded, somewhat oval lobes. Midvein virtually absent; lateral veins thin, repeatedly forked.

Comparisons. *Mariopteris colliciaris* D. White is closely similar to *Mariopteris paddocki* D. White, to which it has been supposed to stand in a varietal relationship (D. White 1943). The pinnules of *M. paddocki* are more slender than those of *M. colliciaris*, however.

There is also a close similarity with *Mariopteris sphenopteroides* Daber which is only marginally different from *Mariopteris colliciaris* D. White by the presence of somewhat larger pinnae and a more slender aspect of the pinnule lobes. It should be

noted that *M. sphenopteroides* Daber is a younger homonym of *M. sphenopteroides* Lesquereux.

Mariopteris beneckeii Huth is also characterized by markedly sphenopteroid pinnules and thus shows a certain resemblance to *Mariopteris colliciaris* D. White. However, *M. beneckeii* has relatively longer pinnules with more angular, sometimes rather pointed lobes which differ clearly from the rounded lobes in *M. colliciaris*.

Mariopteris sphenopteroides Lesquereux (see White 1899) shows relatively broad pinnules with pointed lobes and does not seem nearly as sphenopteroid as *Mariopteris colliciaris* D. White.

Mariopteris loshi (Brongniart) Huth possesses characteristically ovate pinnules (or lobes) which appear somewhat pointed, and thus differ from the more rounded lobes of *Mariopteris colliciaris* D. White.

Remarks. The species described here has been originally recorded as *Mariopteris paddocki* var. *colliciaris* by D. White (1943) in a posthumous work edited by C. B. Read. This paper only contained descriptions and no comparisons. Neither did it state the reasons why *Mariopteris colliciaris* was to be considered a variety of *M. paddocki*, described in the same paper. In the absence of a recorded progression of forms linking *M. paddocki* and *M. colliciaris*, and having regard to the difficulty of determining a varietal relationship in fossil plants, it seems better for the time being to consider both *Mariopteris* mentioned as separate species.

D. White (1943) figured several well-preserved specimens of *Mariopteris colliciaris* from the Lower Pennsylvanian of West Virginia. Especially his plate 13, fig. 5 is directly comparable with the specimen recorded here from the Stephanian B of North-west Spain (Pl. 104, figs. 4, 5; Pl. 105, fig. 3). Despite the great difference in age, as well as the widely separate geographic occurrence, there is such a complete correspondence in morphological features that identification of the Spanish material with the American species is inevitable.

White (1943) noted in the plate explanation (pl. 13) that 'except for the common heteromorphy of the basal pinnules, this form' (*Mariopteris paddocki* var. *colliciaris*) 'is similar to species here described under the genus *Diplothuema*'. This is undoubtedly a reference to the group of *Sphenopteris obtusiloba* Brongniart which is recorded in White's paper under the name of *Diplothuema*, together with other *Sphenopteris* species. It is a fact that the rather stiff, rounded lobes of *Mariopteris colliciaris* evoke the image of certain species of the alliance of *S. obtusiloba*, in particular *Sphenopteris rotundiloba* Němejc (*non* Danzé) and *Sphenopteris whitii* Bell. Also the grooved, slender rachides of *M. colliciaris* are characteristically found in this group of *Sphenopteris*. On the other hand, the presence of transverse bars on the rachides (indistinct though they may be) is a characteristic trait of *Mariopteris* of the group of the *Lineae* (Danzé-Corsin 1953). The presence of bilobate basal pinnules is an even more convincing argument in favour of attributing this species to *Mariopteris* rather than to *Sphenopteris*.

Among the various figures of *Mariopteris* recorded in the literature, two fragments illustrated by P. Corsin (1932, pl. CVII, figs. 1–2) under the name of *Mariopteris rotundata* Huth appear rather similar to *Mariopteris colliciaris* D. White. The pinnules of Corsin's specimens are sphenopteroid to a high degree and thus apparently differ from the predominantly pecopteroid pinnules of the type *M. rotundata* as figured by

Huth (1912, figs. 1–3). Corsin also observed that his specimens appeared more sphenopteroid than the types. Furthermore, it is noted that Huth described the rachides of *M. rotundata* as finely punctate, whereas Corsin described them as possessing faintly marked transverse bars. These differences seem to make Corsin's identification of *M. rotundata* Huth somewhat doubtful. With regard to *M. colliciaris*, it seems that Corsin's specimens show relatively larger pinnules which may be almost twice the size of those belonging to D. White's species.

The specimen of *Mariopteris colliciaris* figured in the present paper represents the only example of *Mariopteris* found in the Villablino coalfield, despite the fact that this coalfield has been exhaustively sampled in recent years. The Villablino coalfield contains measures of Stephanian B and lower Stephanian C ages (compare Wagner 1964, table V). *M. colliciaris* was collected by Dr. W. F. M. Kimpe (Geologisch Bureau, Heerlen) in the course of a detailed stratigraphic investigation of the Villablino coalfield which was carried out in the years of 1953 to 1957. It was obtained from the tip of seam 6 in the mining section of Carrasconte (Kimpe loc. 203), where it occurred in association with the following species (after identifications by R. H. Wagner and, where stated, by the late Professor W. J. Jongmans): *Pseudomariopteris ribeyroui* (Zeiller) Danzé-Corsin, *Dicksonites* cf. *pluckeneti* (von Schlotheim) Sterzel, *Pecopteris feminaeformis* (von Schlotheim) Sterzel, *Pecopteris* (*Ptychocarpus*) *unita* Brongniart, *Pecopteris jongmansii* Wagner, *Polymorphopteris villablinensis* Wagner (representing the higher parts of the frond of *Polymorphopteris subelegans* (Potonié) Wagner?), *Acitheca* sp., *Taeniopteris jejuna* Grand'Eury, *Sphenophyllum oblongifolium* (Germar et Kaulfuss) Unger, *Sphenophyllum longifolium* (Germar) Goeppert, *Sphenophyllum thoni* von Mahr, *Annularia sphenophylloides* (Zenker) von Gutbier, *Annularia stellata* (von Schlotheim) Wood, *Calamostachys tuberculata* Sternberg, *Asterophyllites equisetiformis* (von Schlotheim) Brongniart, *Calamites schutzei* Stur (Jongmans det.), *Calamites* cf. *schutzeiformis* Jongmans et Kidston (Jongmans det.), *Lepidodendron gaudryi* Renault (Jongmans det.), *Sigillaria brardi* Brongniart *formae diversae*, *Sigillariostrobus* sp. The assemblage is one of either late Stephanian B or Stephanian C age. However, additional species recorded from the numerous localities explored by Dr. Kimpe in the Carrasconte area, indicate late Stephanian B rather than Stephanian C. They include the following elements, as identified by one of the present writers (R. H. W.): *Neuropteris ovata* Hoffmann var. *grand'euryi* Wagner, *Cyclopteris fimbriata* Lesquereux (= *Cyclopteris* of *N. ovata*), *Callipteridium* (*Eucallipteridium*) *zeilleri* Wagner, *Alethopteris* cf. *pennsylvanica* Lesquereux, *Alethopteris pseudobohemica* Wagner, *Pseudomariopteris busqueti* (Zeiller) Danzé-Corsin, *Dicksonites pluckeneti* var. *sterzeli* Zeiller, *Sphenopteris matheti* Zeiller, *Sphenopteris* ('*Pecopteris*') *leptophylla* Bunbury (= *Ovopteris pecopteroides* Landeskroener), *Pecopteris arborescens* (von Schlotheim) Brongniart, *Pecopteris hemitelioides* Brongniart, *Pecopteris melendezi* Wagner, *Lobopteris corsini* Wagner, *Polymorphopteris polymorpha* (Brongniart) Wagner, *Polymorphopteris subelegans* (Potonié) Wagner, *Polymorphopteris multifurcata* Wagner, *Lepidodendron* cf. *scutatum* Lesquereux, *Asolanus camptotaenia* Wood, etc.

Occurrence. North America: lower railway cutting, below second sandstone below Raleigh Sandstone (360 ft. below Raleigh Sandstone), Nuttall, West Virginia, U.S.A. (White 1943). North-west Spain: upper Stephanian B, tip of seam 6 of the

Carrasconte mining section of the Villablino coalfield, province of León (Kimpe, loc. 203).

DISCUSSION ON THE PRESENCE OF *MARIOPTERIS* IN STEPHANIAN STRATA

The description of three species of *Mariopteris* from rocks of upper Stephanian B and lower Stephanian C ages in North-west Spain clearly disproves the notion that this genus became extinct at the end of Westphalian or, at the latest, at the beginning of Stephanian times. Of particular interest is the fact that the specimens described here are either identifiable with or closely comparable to Westphalian species of *Mariopteris*. Although the paucity of material (only five specimens among the many thousands collected) indicates that a formerly abundant element of Upper Carboniferous floras has become exceedingly scarce during Stephanian times, the presence of three different species proves its comparative diversity at a time considerably later than that represented by the main occurrence of this group of pteridosperm foliage.

The often repeated statement that *Mariopteris* would be absent from Stephanian strata has thus been proved incorrect. It may, however, be worth while to explore the inadequacy of this statement a little further. In his famous description of the Stephanian flora of Commentry, in Central France, Zeiller (1888) recorded three species of Mariopterid characteristics, viz. '*Diplotmema*' *ribeyroni*, '*Diplotmema*' *busqueti*, and '*Diplotmema*' *paleau*. These species were assigned to *Diplotmema* by Zeiller because they apparently possessed bipartite fronds. However, Danzé-Corsin (1953) observed that the frond was probably quadripartite in *D. paleau*, as was generally the case for *Mariopteris*. She also drew attention to the relatively entire, little lobed pinnules of these three species, and mentioned the presence of bilobate basal pinnules which is a characteristic feature of *Mariopteris*. The foliage of *Diplotmema* in the more restricted sense (Danzé-Corsin 1953) is more highly dissected. Previously, Bell (1938) had already referred '*Diplotmema*' *ribeyroni* Zeiller to *Mariopteris* (with an interrogation mark), whilst Teixeira (1939) described a species of the same alliance under the name of *Mariopteris corsinii* Teixeira. Furthermore, Stockmans and Mathieu (1939), when describing an East Asian species closely similar to '*Diplotmema*' *busqueti* Zeiller, assigned it to *Mariopteris*? *hallei* Stockmans et Mathieu.

As the result of the considerations mentioned above, Danzé-Corsin (1953) decided to receive the three species described by Zeiller in a special genus called '*Pseudomariopteris*'. This genus would be characterized by bipartite or quadripartite fronds with longitudinally striate axes and generally little lobed, almost entire pinnules, as well as bilobate basal pinnules to the pinnae of the last order. Only the presumed predominance of bipartite, instead of quadripartite fronds in *Pseudomariopteris* would distinguish this genus from real *Mariopteris*. The question automatically arises whether such a difference would be adequate to warrant the recognition of a special genus. However, Danzé-Corsin (1953) did include *Pseudomariopteris* with the family of the Mariopterideae (altered to Mariopteridaceae by P. Corsin 1961).

The genus *Pseudomariopteris* gained almost immediate acceptance in the literature and, in fact, provided a most convenient heading for Mariopterids of Stephanian age. Apart from the three species originally described by Zeiller, the more recently described

Mariopteris corsini Teixeira was referred to *Pseudomariopteris* by Wagner (1962, pl. 33) and, ultimately, Alvarez-Ramis and Doubinger (1965) introduced still another species, *Pseudomariopteris villablinensis*. It is to be noted that *Pseudomariopteris ribeyroni* and, to a somewhat lesser extent, *Pseudomariopteris busqueti* are common elements of Stephanian B and C floras. *Pseudomariopteris ribeyroni* has its first occurrence in Westphalian D strata, but does not really become common before Stephanian B.

Stockmans and Mathieu (1957, p. 17) expressed doubt as to the wisdom of recognizing *Pseudomariopteris* as a genus separate from *Mariopteris*, and it may perhaps be considered an open question whether or not *Pseudomariopteris* should be incorporated with the latter. However, there can be no doubt that Mariopteridaceae of a type closely similar to ordinary *Mariopteris* are among the common constituents of Stephanian floras. The general persistence of this group of Pteridosperms is further underlined by the find of three undoubted species of *Mariopteris* in Stephanian B–C rocks, as reported in the present paper.

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NOMENCLATURAL NOTE

CORRECTION OF NAME FOR A DEVONIAN MEGASPORE

SINCE we prepared our paper on the Devonian megaspores from the Wyboston Borehole (Mortimer and Chaloner 1967), we have learnt that the name *Heliosporites* is preoccupied. It was used by Schulz for a genus of Liassic miospores (Schulz 1962).

Wybostisporites nom. nov. is here proposed as a substitute name for *Heliosporites* Mortimer and Chaloner 1967 *non* Schulz 1962. The type species is *W. variabilis* comb. nov.

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Typescript received 5 July 1967

PALAEONTOLOGICAL ASSOCIATION

Notes for Authors submitting papers for publication in

PALAEONTOLOGY

Scope of journal. Papers will be published on **any** aspect of palaeontology; they should be of more than local interest, and they should be written in the English language.

Submission. Typescripts should be sent to the Secretary of the Publications Committee:

N. F. Hughes
Department of Geology,
Sedgwick Museum, Downing Street,
Cambridge, England.

Two complete copies of the typescript (including all explanations of illustrations) should be submitted; photocopies of all text-figures (correctly reduced) and of all plates, should accompany each typescript. The original figures (if they are small) may if necessary serve as illustrations for one copy. Although failure to provide two copies will usually result in slower handling, no paper will be rejected for this reason.

PUBLICATION POLICY OF THE PALAEONTOLOGICAL ASSOCIATION

'*Palaeontology*' provides full opportunity for illustration, but to compensate for the cost of this, **special attention to brevity** is required in the composition of the text. The style should be simple and care should be taken to avoid long complicated sentences so that papers may be read easily by those unaccustomed to the English language.

Classification of papers. Papers will be classified and handled as follows:

(a) Normal papers—less than 25 printed pages of text. Present target for publication is not more than 12 months from submission; this time does not include any delays due to major referee criticism.

(b) Long papers—authors are advised to consult the Editors before submission. Such papers may be delayed while the Association attempts to seek financial support, if the author has not already arranged it.

This statement is intended only as an explanation of intention, and should not be taken as any kind of guarantee; the ultimate control is the available finance of the Association.

Editorial work, correspondence, and delay will be reduced to a desirable minimum if authors will follow these notes carefully.

[*Palaeontology*, Vol. 10, Part 4, 1967, pp. 707–12]

THE TEXT OF THE PAPER

Style and arrangement. Authors should consult published volumes of 'Palaeontology' and construct their papers in accordance with the practices used there, particularly in the arrangement of headings and in the explanations of plates and of text-figures. Numerals are printed in arabic figures. Synonymies should be in a commonly accepted form; the recommended form is:

1947 *Beltanella gilesi* Sprigg, p. 218, pl. 6, fig. 1.

1949 *Beltanella gilesi* Sprigg; Sprigg, p. 81, pl. 10, fig. 1.

Typing. Papers should be typed on good quality paper, preferably of International A4 (29.7×21 cm.) or of quarto size (approx. 10×8 inches or 25×20 cm.). Double spacing of lines (not $1\frac{1}{2}$) is required **throughout** (including references and explanations of plates and text-figures), and there should be a wide margin. Headings should not be underlined, and **nothing should be underlined in running text without good reason**; generic and specific names should be underlined for italic type-setting. Lower case letters are used in English words, except for proper names. In the text references should be cited by the author's name, followed by the date in brackets and by page references where necessary.

Examples:

Cox (1963); Cox (1963, p. 20); (Cox 1963).

The Title should be short and should include fossil group, age and locality.

An Abstract of not more than 200 words is required at the beginning of all papers. It should summarize results (rather than contents) of the paper and should mention new systematic names erected; it should be carefully prepared so that it will serve satisfactorily for international use in abstracting journals.

Footnotes. These will only be allowed in **exceptional** circumstances. Permission to publish, for instance, should be included with other acknowledgements.

References should be arranged in alphabetical order of authors' names at the end of the paper. The author's name should be followed by the year of publication, and the title of the paper in full. The name of the journal (which will be printed in italics) should be abbreviated in the form of the latest edition of the '*World List of Scientific Periodicals*', London. Volume number, part or fascicule number in brackets (only if really necessary), pagination, and number of plates, should be given in arabic figures with the items separated by commas only. For books the title is underlined for printing in italics, and the place (town of publication) should be given. When a reference has been translated or transliterated, the language of origin should be stated in square brackets at the end.

Examples:

BELL, C. W. 1941. Cambrian brachiopods from Montana. *J. Paleont.* 15, 193–255, pl. 28–37.

GOTHAN, W. and WEYLAND, H. 1954. *Lehrbuch der Paläobotanik*. Berlin.

SAMOILOVITCH, S. R. *et al.* 1961. Pollen and spores of Western Siberia. *Trud. vsesoyuz. nauch.-issled. geol. res. Inst., Leningr.* 177, 657 pp., 84+65 pls. [In Russian.]

Text-figures. Originals for text-figures should be submitted drawn in black on good quality white card such as 'Bristol board'. Other materials may be acceptable, but authors using them should assess the risks of distortion. Photo-copies are not usually suitable for reproduction. The original drawings should preferably be made twice the size finally required, and should be of such size that when reduced they will not exceed the type area of a page, $7\frac{1}{2}$ by $5\frac{1}{2}$ inches (19 by 14 cm.). If the caption (explanation) of a full-page figure is long, allowance for its inclusion on the same page should be made by cutting down the (reduced) height of the figure appropriately. In composing smaller text-figures, space on the page is best used if the figure is wide rather than high, and the full width of the page ($5\frac{1}{2}$ inches) should be used if possible. All lettering should be inserted by the author, and special care should be taken to see that it is readable when reduced.

Tables are expensive to set in type if vertical ruling is required and especially expensive if larger than page size; if a table larger than page size is essential it should be arranged for two facing pages or as a horizontal folder. As far as possible all tables of more than two or three lines should be prepared (by careful stencilling) for direct (photographic) line-block reproduction. A photocopy at the correctly reduced size should accompany each copy of the typescript.

Explanations of text-figures, tables, and plates should be typed (double-spaced) and placed at the end of the typescript.

PLATES

Plates will normally be reproduced by the collotype process, but when the amount of detail or nature of the prints or background does not warrant this, a half-tone block may be used.

Making-up. Plates should be submitted with the photographs printed on glossy paper and mounted on strong card which should be kept flat and clean. Prints mounted on a tough thin card survive transit by mail better than on thick card; the original plates should be protected by thin paper overlays. The protective wrapping around the whole package should be thick.

Plates should be assembled after careful study of the methods and detailed notes given below; no plate-space should be wasted. If there is any doubt about method, a mock-up should be sent to the Editors for comment before submission. Figures should always be arranged as close together as they will reasonably go, using the full area of the $8 \times 5\frac{3}{4}$ inch frame. Lines should not be drawn around the plate, or between figures to indicate groupings.

Size. The size of the printed plates is 8 by $5\frac{3}{4}$ inches (20.3×14.6 cm.), excluding the margins. Originals should be of this size, as there is normally little or no advantage in reduction; the Editors should be consulted before submission of originals which exceed $\times 1\frac{1}{2}$. Half-plates may be acceptable; they should be of full width ($5\frac{3}{4}$ inches) and 4 inches (10.15 cm.) high.

Lighting. Where possible, the convention of lighting the fossils from the top left should be followed.

Collotype plates

Contrast. During the collotype printing process contrast is increased, so that in preparing plates for this process prints with excessive contrast should not be used; full black and white tones should not be present. All prints on a plate should be matched for degree of contrast. Relatively soft prints of fossils coated with ammonium chloride reproduce well and are recommended.

Methods of mounting prints. Although a few plates in past volumes of the journal were experimental, most plates were mounted by one of three acceptable methods:

1. *Aligned rectangular prints.* Mount accurately trimmed rectangular prints close together with edges parallel and carefully aligned. The plate-maker will (a) only block out the intervening narrow strips on his negative so that they appear white on the plate, and (b) insert figure numbers in type either below the prints in these strips (leave sufficient space), or in a small cut-out (normally in the bottom right-hand corner).

This method is best for rectangular photomicrographs, and in cases where further print trimming is undesirable. It avoids the possibility of misunderstanding in blocking-out.

Examples:

Vol. 9, Part 2, Pl. 43–47; Vol. 10, Part 3, Pl. 52.

2. *Fossils on cleared background.* Mount the prints (any shape) reasonably close together to avoid waste of space, but do **not** trim prints too close to nor parallel to the edges of the fossils; do not draw a thin black line round the trimmed outline. The plate-maker will block out to the actual edges of all the fossils or rock matrix, and insert figure numbers in type. The plate background will thus be paper white. This method is suitable for many kinds of macro-fossils, but some responsibility for outline is left to the plate-maker.

Examples:

Vol. 9, Part 1, Pl. 13; Vol. 9, Part 2, Pl. 13; Vol. 10, Part 1, Pls. 19–20.

3. *Untouched clean card background.* Mount the prints on very white card (or a sheet of white glossy photographic paper, developed out), kept absolutely clean (no pencil marks, traces of adhesive, etc.). Prints should be trimmed very carefully up to the actual edges of the fossils, or as required. No blocking-out will be attempted, and the original white background will reproduce as a faint grey; figure numbers will be over-printed as before. This method should be used where there is any labelling with directing lines and lettering around the fossil; setting labelling correctly in type is time-consuming and expensive.

Examples:

Vol. 6, Part 1, Pl. 22; Vol. 7, Part 4, Pl. 87.

Combination of methods on one plate may be acceptable, if suitably arranged.

Examples:

Vol. 9, Part 2, Pl. 32; Vol. 10, Part 1, Pl. 10, and Part 4, Pl. 105.

Figure numbers will be overprinted on the plates. They should be inserted clearly, in the final positions (not opposite the centres of the figures) on the protective overlay, and if desired (in methods 1 and 2 only) lightly in pencil in the correct positions on the original plate.

Magnification. The magnification of each figure should be stated in the plate explanation. **Linear scales** are difficult to set in type in the blocked-out areas in Methods 1 and 2 and should be either (a) drawn on a suitable part of the print, or (b) drawn separately on very white card which will be treated as a print (resulting background—faint grey). In Method 3, linear scales may be inserted where required.

Black backgrounds are **not** suitable for the collotype process which is designed to reproduce continuous tone variation. It is very difficult in this process for the printer to maintain a true black and at the same time keep good tone control on the photograph reproduced.

Half-tone plates

Contrast. The photo-engraver will reproduce what he is given; prints should be slightly on the soft side, as contrast can be increased but not reduced. Prints are required; negatives are not suitable.

Mounting. Methods 1 and 2 (above) are suitable, but white backgrounds will appear slightly grey.

Example:

Vol. 6, Part 1, Plate 20.

Black backgrounds are suitable for this method of reproduction, but they should be uniform in shade and the print edges should be made indistinct. White figure numbers and lettering should be stencilled on the black background; as reduction may improve the appearance of the lettering there is some advantage here in constructing plates $\times 1\frac{1}{2}$.

Example:

Vol. 5, Part 2, Pls. 40, 41, 43, 45 (but 42, 44 are collotypes).

Explanations of all plates should be typed (double-spaced) in journal style and placed at the end of the typescript text; repetition of names etc. should be avoided. Magnifications should be stated.

ADMINISTRATION

Preservation of types and other specimens. In accordance with recommendations of the International Codes of Botanical and Zoological nomenclature, these should be in the collection of a reputable institution. The registered numbers should be quoted.

Proofs. Authors will normally receive one proof; this proof is for the purpose of correcting printing errors and not for altering the wording or substance of the paper. Authors will be charged for excessive alterations. The Editors will only be responsible for author corrections notified by return of post. Plate proofs will not normally be sent to authors.

Offprints. Twenty-five offprints of each paper will be sent free of charge, and authors may purchase further copies at prices shown on an order form which will be sent to the author (or corresponding author) when a paper is accepted. A plate surcharge is made on very large orders (over 325 total).

GRANTS IN AID OF PUBLICATION

Authors are requested to seek grants in aid of publication from their institutions or from research funds, or to apply for publication costs in research grants; this is particularly necessary for long papers.

Although acceptance of a paper for publication will not be dependent on the receipt of such grants, authors will appreciate that the funds available to the Association are limited. Every grant or donation therefore will directly help the Association to publish more.

*Prepared by the Publications Committee
The Palaeontological Association*

LONDON

April 1967

THE PALAEOONTOLOGICAL ASSOCIATION

Extracts from the Annual Report of the Council for 1966–7

As the Association enters its eleventh year of development, the decision has been made to publish a new series entitled *Special Papers in Palaeontology*, the first number of which is to be published in 1967.

MEMBERSHIP. On 31 December 1966 there were 1,338 members (703 Ordinary, 118 Student, and 517 Institutional), a net decrease of 4 members during the year. The modest increases in Ordinary and Student membership are similar to those of the previous year and the apparently unfavourable total results from a decline in Institutional membership. This is due to an unusually high number of suspensions of Institutional members in arrear with subscriptions. A substantial number of these have been paid through one specific bookshop and no doubt the Association will eventually retrieve the lost income by other arrangements.

FINANCE. During 1966 income from subscriptions rose by £630, largely because of the increased subscription rate for Institutions and to a lesser extent by an increase in the number of Ordinary and Student members. The increased income fell short of expectations because of non-payment of Institutional subscriptions referred to above.

Sales increased slightly and should continue to rise; offprint sales are now accounted for separately for the first time. Interest from investments is £44 less than in 1965 but the 1966 figure does not include recoverable income tax paid on interest from Liverpool Corporation and Wagon Investments, and a payment of £76 (tax deducted) from Wagon Investments arrived too late to be included. Donations to the General Publication Fund are less than in previous years; tax has still to be recovered on the covenanted subscription from Burmah Oil. The need for these generous donations continues and the Shell Oil Company have kindly donated £250 to help the publication of the Special Papers and have promised continued support. The National Coal Board donation of £1,500 was made specifically towards the cost of the first of the Special Paper Series.

Administration costs are about the same; the smaller figure in the accounts is due to setting the cost of distributing sales against sales income. The cost of publishing *Palaeontology* again rose in 1966 because of increased printing costs. The size of Volume 9 was slightly reduced.

It was necessary in 1966 to make provision for paying for Special Papers and for reprinting, and by transferring sums to meet these needs the Publications Reserve has been reduced to £5,141, enough to cover 63 per cent of the cost of a single volume.

'PALAEOONTOLOGY'. The four parts of Volume 9 were published during 1966. They contained 44 papers.

MEETINGS. Four meetings took place during 1966–7. The Association is grateful to the Council of the Geological Society of London, Professor P. C. Sylvester Bradley (University of Leicester), and Professor J. Sutton (Imperial College, London) for generously granting facilities for meetings, and to the Local Secretaries for their efficient services.

- a. The *Ninth Annual General Meeting* was held in the Rooms of the Geological Society of London, Burlington House, London, W.1, on Wednesday, 2 March 1966, at 5.00 p.m. The Annual Report of the Council for 1965–6 was adopted and the Council for 1966–7 was elected. Professor Marcel Florkin of the University of Liège delivered the *Ninth Annual Address* on 'Palaeo-biochemistry'.
- b. A *Field Demonstration Meeting* was held at Faringdon, Berkshire, on Saturday, 7 May 1966. The theme was 'The Lower Greensand of Faringdon, Berkshire' and the meeting was organized by Mr. S. Locke, Mr. R. V. Melville, and Dr. W. S. McKerrrow.
- c. A *Joint Symposium Meeting* of the Systematics Association and Palaeontological Association was held in the Department of Geology, University of Leicester, on Wednesday–Friday, 21–23 September 1966. The Symposium was entitled 'Tethys, an Ancestral Mediterranean (the evolution of a biogeographic region)'. Dr. T. D. Ford was Local Secretary.

d. A *Demonstration Meeting* was held in the Department of Geology, Imperial College, London, S.W. 7 on Saturday, 10 December 1966, at 2.30 p.m. There were 53 exhibits. The Local Secretary was Dr. Gwyn Thomas.

COUNCIL. The following were elected members of the Council of the Association for 1966-7 at the Annual Meeting on 2 March 1966: *President*: Professor T. S. Westoll, F.R.S.; *Vice-Presidents*: Dr. W. S. McKerrow, Professor F. H. T. Rhodes; *Treasurer*: Dr. C. Downie; *Secretary*: Dr. C. H. Holland; *Assistant Secretary*: Dr. J. M. Hancock; *Editors*: Mr. N. F. Hughes, Dr. Gwyn Thomas, Dr. I. Strachan, Dr. M. R. House; *Other members*: Professor P. M. Butler, Mr. M. A. Calver, Dr. G. Y. Craig, Miss Grace Dunlop, Mr. G. F. Elliott, Dr. T. D. Ford, Dr. B. M. Funnell, Dr. R. P. S. Jefferies, Dr. G. A. L. Johnson, Dr. F. A. Middlemiss, Dr. W. D. I. Rolfe, Professor Scott Simpson, Dr. A. H. Smout, Dr. L. B. H. Tarlo.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1966

BALANCE SHEET

	£	s.	d.	£	s.	d.
<i>Liabilities</i>						
Publications Reserve Account Balance as per Accounts				5,141	7	11
Special Papers Fund				1,385	10	0
Provision for Reprinting				500	0	0
Amounts received in advance of Subscriptions for 1967				396	18	11
Sundry Creditors				28	16	6
Provision for cost of publication of <i>Palaeontology</i> , Vol. 9 as per Income and Expenditure Account	8,047	5	10			
Less expenditure incurred to December 31, 1966	4,818	8	10			
					3,228	17 0

Note. No amount has been included in these Accounts for Subscriptions unpaid at 31 December 1966.

£10,681 10 4

Assets

Office equipment				18	0	0
Investments at cost:						
Equities Fund for Charities—958 units	999	18	3			
5 per cent Defence Bonds	4,000	0	0			
Liverpool 6½ per cent bonds	1,500	0	0			
Wagon Investment Loan 6¾ per cent	2,000	0	0			
					8,499	18 3
Sundry Debtors:						
Authors for offprints				179	11	9
Advance Payments:						
For <i>Palaeontology</i> , Vol. 10	630	12	0			
For <i>Palaeontology</i> , offprints	87	5	0			
					717	17 0
Cash at Bank—Deposit Account				75	19	4
Current Account				1,190	4	0
					£10,681	10 4

Report of the Auditors to the Members of the Palaeontological Association. We have examined the above Balance Sheet and annexed Income and Expenditure Account which in our opinion give respectively a true and fair view of the state of the Association's affairs as at 31 December 1966 and of its income and expenditure for the year ended on that date.

JOSHUA WORTLEY & CO.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT
FOR THE YEAR ENDED 31 DECEMBER 1966

<i>Expenditure</i>	£	s.	d.	£	s.	d.
<i>To</i> Provision for Publication of <i>Palaeontology</i> ,						
Vol. 9, Part 1	1,968	13	5			
Part 2	2,098	7	5			
Part 3	2,000	0	0			
Part 4	1,980	5	0			
	8,047	5	10			
Add extra cost of						
Vol. 8, Part 3	363	3	7			
Part 4	233	3	2			
				8,643	12	7
Administrative Expenses:						
Insurance	2	0	3			
Auditor's Fee	10	10	0			
Post and Stationery	105	1	10			
Assistance for Treasurer	100	0	0			
Duplication and dispatch of circulars	164	17	0			
Meetings	18	6	10			
				400	15	11
Depreciation of equipment				2	15	0
To Special Paper Fund				1,385	10	0
				£10,432	13	6
<i>Income</i>						
<i>By</i> Subscriptions for 1966	5,686	19	10			
Subscriptions for 1965	125	2	5			
				5,812	2	3
Sales of <i>Palaeontology</i>				1,351	2	6
Profit from sales of offprints				30	4	0
Interest received:						
5 per cent Defence Bonds	200	0	0			
Equities Fund for Charities	71	17	0			
Liverpool Corporation	47	13	4			
Wagon Investments	29	1	8			
Deposit Account	18	10	9			
				367	2	9
Specific Donations				124	15	11
General Donations:						
British Petroleum	250	0	0			
Mobil Oil	100	0	0			
Texaco	175	0	0			
Burma Oil	58	15	0			
				583	15	0
Special Papers Donations:						
N.C.B.	1,500	0	0			
Shell Oil	250	0	0			
	1,750	0	0			
Less printing costs	364	10	0	1,385	10	0
Miscellaneous Receipts				128	12	5
Excess of Expenditure over Income transferred to Publications Reserve				649	8	8
				£10,432	13	6

INDEX

Pages 1 to 170 are contained in Part 1; pages 171 to 337 in Part 2; 339 to 523 in Part 3; and 525 to 715 in Part 4. Figures in **Bold Type** indicate plate numbers.

A

- Acanthochitina barbata*, 443, **68**.
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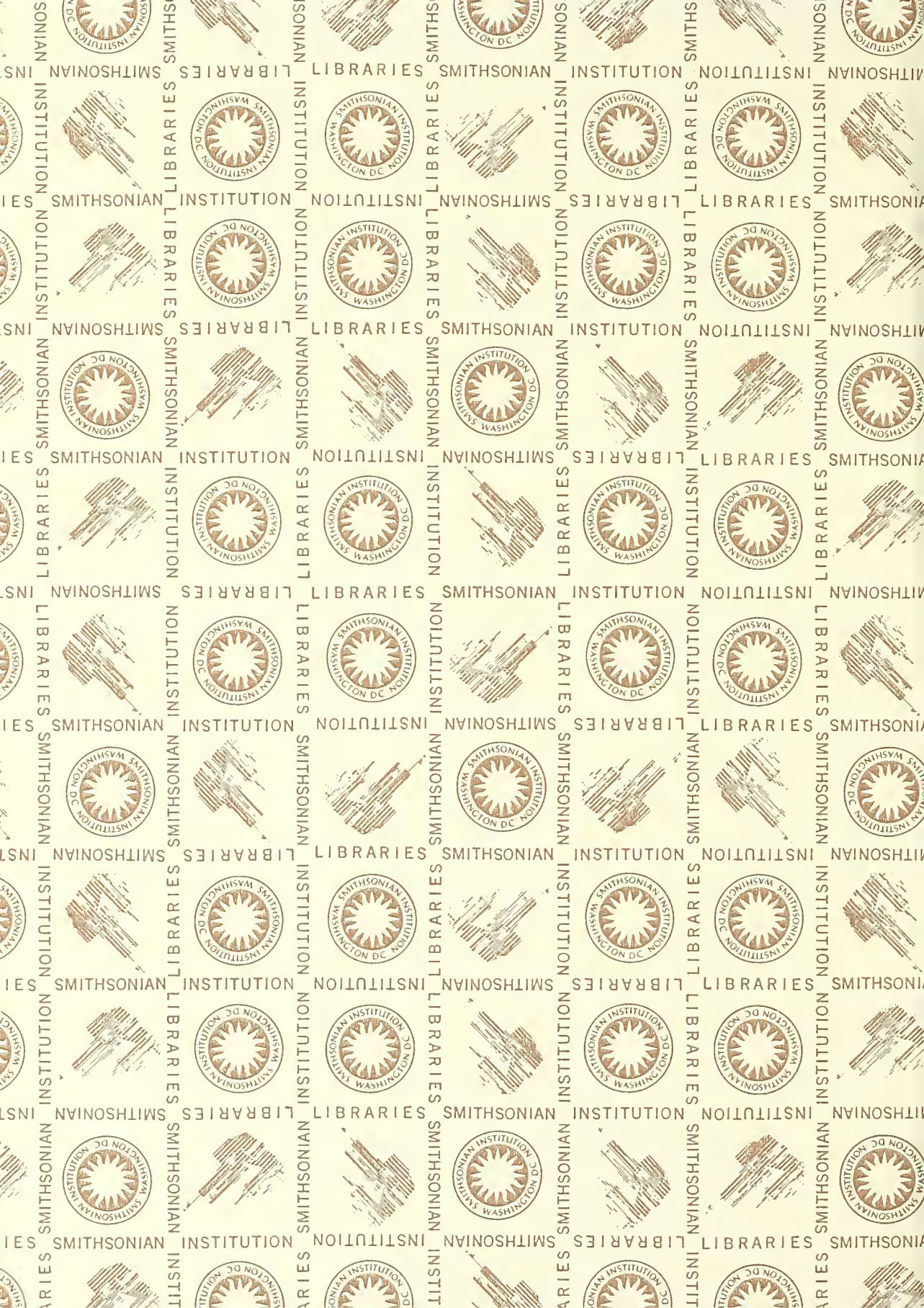
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